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PREDATOR-PREY DYNAMICS BETWEEN MOUNTAIN LIONS AND MULE DEER: EFFECTS ON DISTRIBUTION, POPULATION REGULATION, HABITAT SELECTION, AND PREY SELECTION

A

THESIS

Presented to the Faculty of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements

for the Degree of

DOCTOR OF PHILOSOPHY

By

Becky Miranda Pierce, B.S., M.S.

Fairbanks, Alaska

May 1999

PREDATOR-PREY DYNAMICS BETWEEN MOUNTAIN LIONS AND MULE DEER: EFFECTS ON DISTRIBUTION, POPULATION REGULATION, HABITAT SELECTION AND PREY SELECTION

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ABSTRACT

Mountain lions (*Puma concolor*) and mule deer (*Odocoileus hemionus*), which share a winter range in the Eastern Sierra Nevada in Round Valley, California, USA, were fitted with radio-telemetry collars and tracked to determine their movements and cause of mortality. The mountain lion population of Round Valley refers to a group of individuals that lived in close proximity to one another, essentially isolated from similar groups during the winter, and fed on the migratory herd of mule deer that overwinter in Round Valley. Mountain lions migrated seasonally with the deer population, and two distinct patterns for coping with variability in abundance of prey were observed. The unique migratory behavior identified for the mountain lions in this study indicates a more flexible social system for mountain lions than previously described. Tests of whether the presence of another mountain lion affected where individuals to killed deer indicated that social interactions had no effect and that social behavior was not regulating the population of mountain lions via spatial partitioning of prey. Examination of habitat selection by mule deer and mountain lions revealed that mule deer selected habitat at higher elevations ($P < 0.001$) with more bitterbrush (*Purshia tridentata*) and less rabbitbrush (*Chrysothamnus nauseosum*) than random locations. Mountain lions killed deer in relatively open areas with more desert peach (*Prunus andersonii*) than locations in which deer foraged. Those results indicated that deer were not confronted with a tradeoff in terms of habitat selection on the winter range because habitat with the best forage (e.g. bitterbrush), also provided the least predation risk. Comparisons of mule

deer killed by mountain lions, coyotes, and automobiles indicated that mountain lions selected young (< 1 year old) deer and both predators selected older age classes among adults. Furthermore, there was no selection by either predator for animals in poor condition. Among mountain lions in different social categories, female mountain lions with kittens selected more young deer than did other social categories. This study indicated that ambush predators (mountain lions) may be as selective for prey as coursing predators (coyotes) and that lactation in mountain lions may play a role in determining prey selection.

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ACKNOWLEDGMENTS

This thesis is comprised of four chapters, each of which has been submitted or accepted for publication, with myself as senior author. In chapter one "we" refers to myself, V. C. Bleich, R. T. Bowyer and J. D. Wehausen. For chapters two, three and four, "we" refers to myself, V. C. Bleich and R. T. Bowyer. This study is a contribution from the California Department of Fish and Game (CDF&G) Deer Herd Management Plan Implementation Program and numerous organizations provided additional support. I thank the CDF&G, The National Rifle Association, Friends of the National Rifle Association, The Mule Deer Foundation, Safari Club International (Los Angeles, Orange County, Sacramento, San Fernando, and San Francisco Bay Area chapters), the Fish and Game Advisory Committee of Inyo and Mono Counties, California Deer Association, University of California White Mountain Research Station, and the Institute of Arctic Biology at the University of Alaska Fairbanks. I also thank E. Loft, K. Mayer, S. Mastrup, R. Mohr, B. Schaefer, S. Torres and T. Mansfield for support of this research. Many people contributed expertise in the field and in data analysis. I am extremely grateful to the houndsmen, field technicians, and volunteers that helped capture mountain lions and to locate deer killed by mountain lions: J. Davis, V. Davis, J. Ostergard, C. Baker, P. Partridge, C.-L. Chetkiewicz, G. Raygorodetsky, and D. Stoner. Special thanks to the hounds themselves for their amazing courage and abilities. I am grateful to J. Wehausen for assistance in capturing mountain lions and discussing ideas. I also am grateful to the volunteers who helped in daily monitoring of the deer herd: W. Allsup, C.

Baker, G. Clarkson, H. Jones, R. Noles, D. Noles, N. Partridge, P. Partridge, B. Peters, P. Thompson and, the late, R. Williamson. I am grateful to Dr. T. Stephenson for ultrasonography during deer captures and I thank the many people that assisted in the capture of mule deer. I extend special thanks to the animal capture specialists from the CDF&G Wildlife Investigations Laboratory, especially W. Clark, B. Teagle and B. Knuchols, and S. DeJesus from Landells Aviation for the safe manuevering near the ground. Many thanks to pilot R. Anthes for his safe flying in the mountains and his special effort to get accurate locations. I am grateful to P. Carter for help in the office and radio monitoring. I extend my appreciation to J. A. K. Maier, M. Nicholson and C. Howard, for their help with Arc Info. Thanks to E. Rexstad, V. Van Ballenberghe, and R. G. White, for helpful suggestions with each chapter and J. Kie for financial support and statistical advice. Thanks, also to my fellow graduate students in "the pit" for company during the misery and, especially to M. Oehler for help with lab analyses, truck repair, and furniture moving. I am also grateful to my friends, the Daniels, who provided important emotional support and many meals. My greatest thanks to V. C. Bleich who worked so very hard on all aspects of this research and to whom I owe the opportunity to gain such a great career experience and to R. T Bowyer who was responsible for my surviving the data analysis, writing, and Fairbanks. I thank my parents for their financial support and I thank Taylor Ann and Sonny Boy, my faithful pets, for their companionship; Sonny in particular, for locating deer carcasses and mountain lions, and keeping me safe. Finally, I dedicate this volume to the late Dr. Pamela Wofford, my best

friend of 23 years, without whom I would never have had courage enough to try; may you finally hear a wolf howl.

THESIS INTRODUCTION

Round Valley (37°24'N, 118°34'W), located on the east side of the Sierra Nevada in eastern California, is the winter range for a migratory population of mule deer (*Odocoileus hemionus*) and the mountain lions (*Puma concolor*) that prey upon them. The mountain lion population of Round Valley refers to a group of mountain lions that lived in close proximity to one another, essentially isolated from similar groups during the winter, and feeding on the migratory herd of mule deer that overwinter in Round Valley.

The predominant vegetation association in Round Valley is characteristic of the Great Basin. Bitterbrush (*Purshia tridentata*), sagebrush (*Artemisia tridentata*), and rabbitbrush (*Chrysothamnus nauseosum*) predominate in a mosaic where patches of blackbrush (*Coleogyne ramosissima*) and mormon tea (*Ephedra nevadensis*) are common. The deer inhabiting Round Valley migrate to high elevations (> 2500 m) on the west side of the Sierra Nevada to take advantage of high-quality forage during the dry summer. Mule deer accomplish this crossing by moving north or south of the valley and traversing several passes at elevations > 3,000 m. Deer remain on the summer range until autumn when winter storms push these herbivores back over the crest and down to the valley floor.

The mule deer population wintering in Round Valley declined steadily from about 6,000 (66/km^2) animals in 1985 to < 1,000 (10/km^2) deer in 1991. That decline corresponded with a severe drought and a subsequent reduction in forage availability.

The end of the drought coincided with the beginning of our study in 1991. Following the decline of the deer population in the 1980s, estimated numbers of deer on the winter range increased gradually over the period of the study from 1,344 (15/km^2) in 1993 to 1,913 (21/km^2) in 1997. During that same period, average numbers of adult mountain lions located on the winter range by telemetry flights conducted weekly, plummeted from 6.1 in winter 1992-1993 to 3.0 in 1996-1997.

We studied the mule deer and mountain lion populations that inhabited Round Valley from November 1991 to December 1998. The movements of mountain lions between subpopulations in response to migration by mule deer raised questions about the social organization of those mountain lions, and suggested a more flexible social system than previously described for these solitary felids. Criteria necessary to invoke social behavior as a mechanism for regulating a population were outlined by Watson and Moss (1970) and emphasized by Seidensticker et al. (1973). Their first two criteria required that reproduction be limited in individuals that could otherwise breed if social interactions with conspecifics did not inhibit them from doing so. The third requirement emphasized that resource limitation must be eliminated as a contributing factor, and that mortality or depressed recruitment attributed to social behavior must be inversely correlated with other causes of mortality or depressed recruitment. Although we do not address the potential for mortality resulting from intraspecific aggression to regulate the population of mountain lions in our study because young mountain lions may have been killed without our knowledge, the hypothesis of social regulation in mountain lions,

however, is generally reliant on a scenario where transient individuals are excluded from becoming permanent members of the population regardless of the availability of prey. For this reason we examined the role of social behavior in the acquisition of prey by mountain lions and tested the hypothesis that social interactions could limit a population of mountain lions through territoriality and limited access to prey.

Tests for the effects of social interactions among mountain lions in the acquisition of prey indicated that the distribution of mule deer killed by mountain lions in comparison to the distribution of mule deer throughout Round Valley differed. We hypothesized that mule deer on the winter range did not forage randomly among habitats but selected habitat in response to a predation risk:forage ratio. Furthermore, we hypothesized that mountain lions did not kill deer randomly among the habitats in which they occurred, but selected to kill deer in habitat with significant cover to facilitate stalking of prey. If deer in Round Valley faced a trade-off in their forage benifit:predation risk ratio then mountain lion predation might have an additional effect on mule deer reproduction by limiting access to high quality forage for mule deer on the winter range.

Finally, we tested hypotheses of prey selection between mountain lions and coyotes, and among different social categories of mountain lions. We hypothesized that coyotes, a coursing predator, would exhibit selection for young, old and weak individuals whereas mountain lions, which ambush prey, would not be able to select among age class, sex or condition of mule deer they killed. Furthermore, we hypothesized that, because

mountain lions were much larger than coyotes, they would have less tendency to be selective for small prey than coyotes. Finally, we tested the null hypothesis that different social categories of mountain lions did not differ in selection of prey. Thus, this thesis integrates the ecology and behavior of both mountain lions, and their primary prey, mule deer, to answer questions concerning predator-prey dynamics of large, vagile mammals.

[1]CHAPTER 1.

MIGRATORY PATTERNS OF MOUNTAIN LIONS: IMPLICATIONS FOR SOCIAL REGULATION AND CONSERVATION

We studied movements of mountain lions (*Puma concolor*) in the southern Sierra Nevada of California from 1992--1997. We observed two distinct patterns, which likely represent strategies of mountain lions for coping with variability in abundance of their primary prey, mule deer (*Odocoileus hemionus*). Some mountain lions migrated together, often slowly, following movements of mule deer from winter range toward the summer range of their prey. Those mountain lions remained together on the eastern scarp of the Sierra Nevada and overlapped in distribution throughout the year. Other mountain lions exhibited rapid movements to disjunct summer ranges, on the western side of the Sierra Nevada, shared with mountain lions that did not occur on their winter range. Mountain lions that moved more slowly and overlapped in distribution had large annual home ranges (95% adaptive kernel; $\bar{X}$ = 817 km^2), whereas mountain lions with distinct summer ($\bar{X}$ = 425 km^2) and winter ($\bar{X}$ = 476 km^2) distributions had smaller home ranges. Such disparate patterns of movement may lead to difficulties in sampling population size for mountains lions. Moreover, maintaining corridors that would allow for both patterns

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[1] Pierce, B. M., V. C. Bleich, J. D. Wehausen, and R. T. Bowyer. 1999. Migratory patterns of mountain lions: implications for social regulation and conservation. Journal of Mammalogy, 80:in press.

of movement may be critical for the conservation of these large felids. Finally, extensive overlap in the distribution of mountain lions, especially the association of one group of individuals on winter range and another on summer range for mountain lions with disjunct distributions, indicates a more flexible social system than previously described.

Key words: *Puma concolor*, mountain lion, home range, migration, conservation, behavior, social organization, Sierra Nevada, California

Mountain lions (*Puma concolor*) that feed on nonmigratory populations of ungulates can have distributions and sizes of home ranges that change little over time (Hopkins, 1989; Sweanor, 1990). Nonetheless, populations of mountain lions that feed on migratory mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*) exhibit seasonal movements, particularly elevational shifts, with those primary prey (Anderson et al., 1992; Rasmussen, 1941; Seidensticker et al., 1973). Most periodic movements noted in those studies, however, were gradual, and seasonal home ranges of mountain lions usually remained contiguous. Little attention has been given to the relatively long-range migrations made by some mountain lions within subpopulations or the potential significance of those movements between subpopulations.

Social regulation of mountain lions may occur in populations with high densities of prey as a result of territorial behavior among resident adults (Lindzey et al., 1994; Seidensticker et al., 1973). Those studies proposed that populations of mountain lions

often exhibited a land-tenure system of resident adults that shared space but avoided each other temporally. Hornocker (1969) termed that behavior, mutual avoidance. In those systems, resident adults had overlapping home ranges but did not allow younger mountain lions that were transient to establish residency unless a vacant home range became available. Thus, density of mountain lions was independent of the density of their primary prey (Seidensticker et al., 1973). Such intrinsic limitation of the population, however, is reliant on a system where individual mountain lions are familiar with other conspecifics with which they share space. Under a land-tenure system, spatial arrangement and social behavior of mountain lions would be expected to be relatively stable. For populations of mountain lions that are dependent on a migratory prey base, however, such a social system could pose problems when prey leave an area.

For many species, migratory behavior has evolved in response to seasonal changes in availabilities of habitat and food (French et al., 1989). In ungulates, mixed strategies of migration occur within populations as a result of variation in food availability in different areas among years (Loft et al., 1984; Nicholson et al., 1997). Because populations of deer can comprise individuals with different migratory patterns, mountain lions also may have evolved flexibility in social behavior that allows them to cope with changes in prey density.

Migratory behavior in mountain lions may have important implications for management and conservation of this large felid. Track censuses often have been proposed for mountain lions as a reliable method for detecting trends in population

change (Beier and Cunningham, 1996; Van Dyke et al., 1986; Van Sickle and Lindzey, 1992). An understanding of differences in migration strategies within a population or between subpopulations is imperative for such techniques to provide accurate information.

We quantified timing of migration in mountain lions and tested for differences in size and distribution of their home ranges in summer and winter. In addition, we described several strategies of movement by mountain lions within a single subpopulation and tested for differences in the size of home ranges by animals following those disparate patterns. We also discuss potential implications of home-range dynamics in mountain lions for social regulation and conservation of this solitary carnivore.

MATERIALS AND METHODS

Study area.---Round Valley, located on the eastern side of the Sierra Nevada, a major mountain range in California (37°24'N, 118°34'W), was the winter range for a migratory population of mule deer. Most of those deer migrated to the west side of the Sierra Nevada mountains in spring and returned to Round Valley each autumn (Kucera, 1992). The crest of the Sierra Nevada provided a distinct boundary between the east and west sides of that mountain range, with many peaks >4,000 m above mean sea level. Migration of deer occurred via several mountain passes >3,000 m. Most deer moved to summer ranges over the crest of the Sierra Nevada in mid-June and returned to winter range by mid-November. The White Mountains, ca. 25 km E of Round Valley, also rise to 4,000 m and were inhabited by a resident population of mule deer.

Analyses of home ranges.---We monitored the population of mountain lions associated with the deer herd in Round Valley from February 1992 to October 1997. We captured 21 adult mountain lions using hounds or snares (Davis et al., 1996; Pierce et al., 1998) and fitted them with radiotelemetry collars during November 1991--May 1995. We used a fixed-wing aircraft to locate mountain lions each week. A maximum density of 10 adults (ca. 1 mountain lion/25 km^2) was recorded within the boundary of the study area in 1992--1993. Density of mountain lions was likely highest in winter 1991--1992 before several adults died. These deaths occurred prior to our collaring all known individuals, and we could not confirm their presence on the study area during aerial-telemetry flights; therefore, we did not include that period in our analysis of mountain lion density. All methods used in this research were approved by the Institutional Animal Care and Use Committee at the University of Alaska Fairbanks.

The CALHOME (Kie et al., 1996) program was used to calculate 95% home ranges using the adaptive-kernel method (Worton, 1989) for nine adult mountain lions with locations ($\bar{X}$ = 29.2, SD = 5.8) that spanned ≥12 months. For females that made extensive seasonal movements, we estimated annual home ranges using the first location of an individual on winter range (east side of the Sierra Nevada) through the last location of that individual on summer range (west side of the Sierra Nevada, or in the White Mountains). For some of those females, analysis of home range resulted in separate 95% contours for winter and summer. Therefore, discontinuities between home ranges in winter and summer were not the result of pre-selecting dates but were based on adaptive-

kernel analyses. For instances where mountain lions had disjunct home ranges, we tested for differences in sizes of winter and summer home ranges using the Wilcoxon matched-pairs signed-ranks test (Siegel, 1956).

Some females followed the beginning of the deer migration N but remained on the east side of the Sierra Nevada throughout summer. In most instances, there were not dramatic movements to and from seasonal home ranges, and those females periodically returned to winter range during summer. Because no distinct migrational movements were identified, analyses of annual home ranges were based on the first location obtained in November through the last one recorded in the following October. That period coincided with the arrival of deer on winter range. For periods that did not span 12 months prior to November or following October, data were excluded. Two males also were included in the analyses using the same criterion.

Percent overlap of seasonal home ranges was measured for females that had discontiguous seasonal home ranges on opposite sides of the Sierra Nevada and returned to those home ranges in consecutive years. Percent overlap was calculated as the area of overlap for two consecutive seasonal home ranges, divided by the area of the smallest of the two home ranges. We calculated that measure using 95% contours from 2 consecutive years for one female and 4 consecutive years for the other.

RESULTS

Mountain lions exhibited two distinct patterns of movement in response to migration of mule deer. Some mountain lions moved gradually, remaining on the eastern

scarp of the Sierra Nevada and often having home ranges that overlapped throughout the year. Analysis indicated a single annual home range for those mountain lions. Other mountain lions made two long-range movements each year, also corresponding with the migration of the deer herd. Those mountain lions moved across the crest of the Sierra Nevada or to the White Mountains. Analysis of home ranges for that pattern of movement generally defined two distinct areas, one each for summer and winter. Those mountain lions that crossed the crest of the Sierra Nevada or migrated to the White Mountains likely overlapped with other subpopulations of mountain lions known to inhabit that region of their summer distribution.

Five of nine mountain lions moved north (three females and one male) or south (one male) with the deer herd as it dispersed from Round Valley to summer range. One of those females did not return to the winter range during one summer and had disjunct home ranges in summer and winter. Movements were gradual for four individuals and did not result in discontiguous home ranges between seasons in eight of nine instances; the male that moved southward had distinct summer and winter home ranges in 1 of 4 years. Mean ($\pm$ *SD*) size of annual home ranges was 817 ± 379 km^2. Three female mountain lions followed the migration routes of the deer in spring through high mountain passes, and established summer ranges west of the crest of the Sierra Nevada (Fig. 1.1a,1.1b,1.1d). A fourth female moved eastward in spring after leaving Round Valley and established a home range in the White Mountains during summer (Fig. 1.1c). The

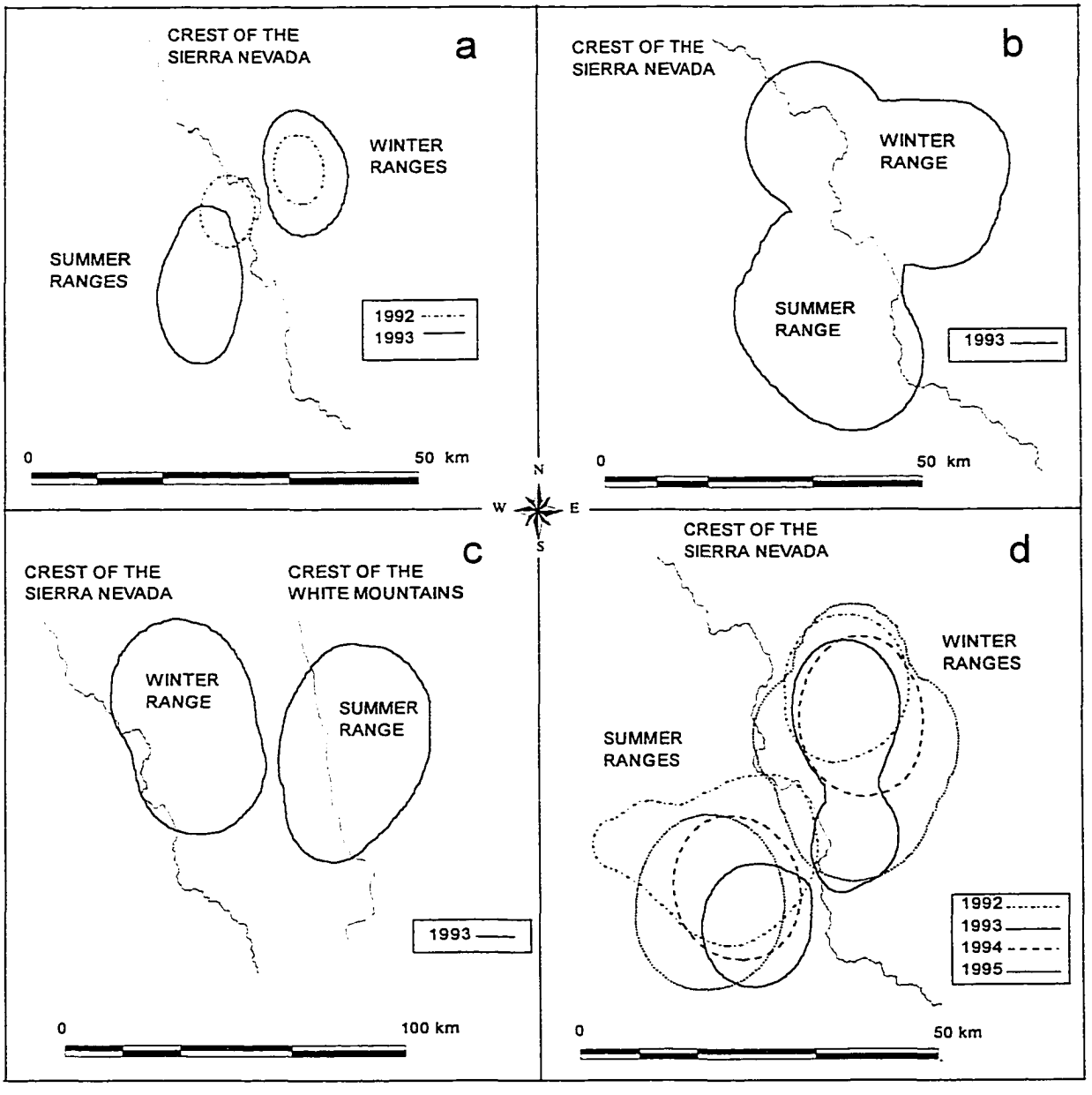

FIG. 1.1---Winter and summer home ranges (95% adaptive kernels) for four female mountain lions (a, b, c, d) that migrated from winter range in Round Valley, California, to summer ranges on the west side of the crest of the Sierra Nevada and the White Mountains. For clarity, only 4 of 6 consecutive years are shown for the female in Fig. 1d.

following year, that female switched her pattern and moved N of Round Valley, had a single annual home range and raised a litter of young (Bleich et al., 1996). That female remained in close proximity to other females inhabiting the east side of the crest of the Sierra Nevada during summer.

Timing of migration by mountain lions corresponded with the migration of mule deer. All four mountain lions that made extensive movements (Fig. 1.1) migrated by July and returned to Round Valley by November every year, except one individual that crossed the crest of the Sierra Nevada in December 1993 and August 1994. Of the three female mountain lions that migrated westward over the Sierra Nevada, two traveled with single male offspring.

Seven of nine migrations of mountain lions over the crest of the Sierra Nevada resulted in winter and summer home ranges that were not contiguous (Fig. 1.1), and movements of those mountain lions occurred after migrations of deer in autumn and spring. Mean ($\pm$ *SD*) size of summer (292 ± 120 km^2) and winter (307 ± 152 km^2) home ranges for two mountain lions with disjunct seasonal ranges on opposite sides of the Sierra Nevada did not differ significantly ($Z = -0.169$, $d.f. = 6$, $P = 0.87$). Mean ($\pm$ *SD*) size of summer (425 ± 475 km^2) and winter (476 ± 465 km^2) home ranges for all mountain lions with disjunct ranges also did not differ ($Z = -0.612$, $d.f. = 9$, $P = 0.54$). The two mountain lions that crossed the crest of the Sierra Nevada and returned to summer home ranges in consecutive years exhibited strong fidelity to home-range in summer and winter (Fig. 1a,1d). Overlap of home ranges was 33% in summer and 100%

in winter for one of those females. Mean ($\pm$ *SD*) overlap for the other female was 71 $\pm$ 15% for summer, and 83 $\pm$ 15% in winter.

Both males included in analyses also remained on the east side of the Sierra Nevada throughout summer. One moved northward and had a single annual home range that overlapped those of the females that remained on the east side. One repeatedly moved southward along the Sierra Nevada and into the Owens Valley adjacent to the east side of those mountains.

Discussion

Our results indicate that mountain lions that depend on migratory prey may have multiple strategies of migration that allow them to cope with changing densities of prey. Mountain lions that wintered with a migratory deer herd on the east side of the Sierra Nevada exhibited two general patterns of movement. Most remained on the east side of the Sierra Nevada during summer, extending their winter range but returning to it periodically throughout the year. Most mountain lions exhibiting that pattern of movement had singular annual home ranges that tended to overlap those of other lions. Because those mountain lions moved together with the herd of mule deer and remained in close proximity to one another, they may not have interacted with mountain lions from other winter ranges. Mountain lions that migrated to the west side of the Sierra Nevada or to the White Mountains tended to make long-range movements that resulted in distinct summer and winter ranges. Three mountain lions that migrated over the crest of the Sierra Nevada and one that migrated to the White Mountains became members of

different subpopulations during summer and winter. Furthermore, the female that migrated to the White Mountains in one summer changed her pattern of movement and overlapped extensively with mountain lions on the east scarp of the Sierra Nevada the following summer. Although sample size of locations was too small for making inferences about home-range sizes for some individuals, our results demonstrated distinct patterns in movement among mountain lions and indicated multiple patterns of migration and flexibility in social behavior in response to changing densities of prey.

Track censuses have been proposed as a meaningful method for estimating trends in populations of mountain lions throughout much of their range (Beier and Cunningham, 1996; Currier, 1976; Koford, 1978; Van Dyke et al., 1986), including the eastern Sierra Nevada (Smallwood, 1994). Where some mountain lions migrate seasonally and others do not, investigators cannot be certain of the population being monitored; survey results also may vary with season and, hence, lead to spurious conclusions. The potential for mountain lions to migrate needs to be considered in planning such surveys.

Knowledge and understanding of migration patterns have fundamental importance for conservation of mountain lions. Migration is an adaptive strategy that likely evolved in response to variability in the environment (Baker, 1978). Multiple strategies, where some segment of a population migrates while another remains resident, have been observed for mule deer (Nicholson et al., 1997), and that same behavior was evident among mountain lions inhabiting Round Valley. Therefore, viability of some populations of mountain lions may rely on seasonally distinct geographic regions that allow

individuals to cope with environmental fluctuations. Furthermore, because migration often requires suitable habitat for movement between seasonal ranges, maintenance of corridors for migration by mountain lions may be essential for maintenance of some subpopulations, as has been suggested for dispersal corridors for mountain lions in southern California (Beier, 1993, 1995, 1996). Moreover, gene flow among populations of mountain lions may be as dependent on patterns of migration of adults as it is on dispersing juveniles. Thus, migratory behavior by this large felid may play a critical role in metapopulation structuring (Levins, 1970).

Several mountain lions repeatedly migrated into areas that they had left vacant for >6 months. During summer, home ranges of those individuals were in areas inhabited by subpopulations of mountain lions that spent each winter in areas isolated from Round Valley (Bleich and Taylor, 1998; Torres et al., 1996). In winter, those individuals reestablished home ranges in Round Valley among mountain lions with which they had not interacted throughout summer. Extensive movements of mountain lions suggest that the social system thought to play a role in regulating populations of mountain lions (Seidensticker et al., 1973) may be far more flexible than previously recognized. Extensive overlap of home ranges of mountain lions occurred on a seasonal basis. Migratory populations of prey and their resultant shifts in density likely caused numbers of mountain lions to fluctuate seasonally.

Factors promoting social regulation (Watson and Moss, 1970) may operate differently in populations of mountain lions that feed on migratory prey compared with

populations where densities of prey do not vary seasonally. In situations such as our study area, mountain lions can reach high densities and potentially have a strong influence on populations of mule deer (Bleich and Taylor, 1998). Research on the potential for social regulation to limit densities of mountain lions must include detailed information about distribution of their primary prey (Anderson et al., 1992). Whether the patterns of distribution for mountain lions we observed can lead to social regulation requires further study, but these patterns certainly raise questions about existing paradigms of social behavior of mountain lions.

ACKNOWLEDGMENTS

We thank the houndsmen and field technicians that helped capture and radio-track mountain lions including J. Davis, V. Davis, J. Ostergard, C. Baker, W. Allsup, C.-L. B. Chetkiewicz, and G. Raygorodetsky. We also thank members of the Air Services Branch of the California Department of Fish and Game (CDFG), particularly R. Anthes, who made extensive efforts to locate lions that migrated. We greatly appreciate the help of C. Howard and M. Nicholson with Geographic Information Systems. This research was supported by the CDFG, University of California White Mountain Research Station, National Rifle Association, Friends of the National Rifle Association, The Mule Deer Foundation, Safari Club International (Los Angeles, Sacramento, San Fernando, San Francisco Bay Area, and Orange County chapters), the Fish and Game Advisory Committee of Inyo and Mono counties, the California Deer Association, and the Institute of Arctic Biology at the University of Alaska Fairbanks. This is a contribution from the

CDFG Deer Herd Management Plan Implementation Program, and is professional paper 007 from the Eastern Sierra Center for Applied Population Ecology.

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[2]CHAPTER 2

SOCIAL ORGANIZATION OF MOUNTAIN LIONS:

DOES A LAND-TENURE SYSTEM REGULATE POPULATION SIZE?

Abstract. Mountain lions (*Puma concolor*) are thought to regulate their populations via social behavior. The proposed mechanism is a land-tenure system that results in exclusion of individuals from the population through intraspecific aggression or mutual avoidance. In the absence of mortality from intraspecific aggression, social behavior can regulate a population only by limiting reproduction. Hence, several predictions can be made for a population that is regulated by social behavior via a land-tenure system: 1) individuals should not be distributed randomly but each should have its own distinct distribution, and these individuals should maintain regions of exclusivity; 2) the use of food resources within the distribution of an individual should not be random, but should be clumped as individuals try to exclude each other from access to prey; 3) these clumps of prey must not be simply the result of prey distribution but of social interactions; and 4) social interactions and defense of food resources should occur in regions where distributions of individuals overlap; therefore, prey use by individual lions in areas of overlap should be less than expected based on the distribution of prey.

We tested hypotheses regarding social regulation for a group or "population" of

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mountain lions that co-occurred, on a winter range with a population of mule deer (*Odocoileus hemionus*) in the eastern Sierra Nevada, California from 1991 to 1997. Individual mountain lions ($n = 10$) exhibited distinct distributions, and deer killed by individuals ($n = 112$) were not randomly distributed within the distribution of the lion that did the killing. Furthermore, the nonrandom distribution of lion-killed deer could be explained by the distribution of deer alone, but this result was marginally not significant ($P = 0.06$) and suggested that something else affected the location of kills made by lions. Results of tests of whether the presence of another mountain lion affected where individuals chose to kill prey indicated that social interactions had no effect. The distribution of deer killed by individual mountain lions in areas of exclusive use and areas of overlap was identical to what was expected based on the distribution of deer alone. This outcome indicated social behavior was not regulating the population of mountain lions via partitioning of prey, and that temporal differences in use of space could not explain the distribution of mountain lions we observed.

Key words: Puma concolor, Odocoileus hemionus, *predation, social behavior, land-tenure, population regulation.*

INTRODUCTION

Social behavior and organization has been proposed as a mechanism for regulating populations of mountain lions (*Puma concolor*). Hornocker (1970) indicated that numbers of mountain lions did not increase with increases in populations of mule

deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*), suggesting that territoriality limited the population of mountain lions independent of prey density. Further investigation of this same population lead to the hypothesis that mountain lions exhibited a land-tenure system where individuals used common areas but separated temporally by maximizing distances between individuals through visual and olfactory cues (Seidensticker et al. 1973). Indeed mountain lions can be territorial and resulting aggression often leads to death of conspecifics (Anderson et al. 1992). Population density was thought to be limited because individuals could not establish residence unless a home area became vacant (Seidensticker et al. 1973). This behavior, termed "mutual avoidance" (Hornocker 1969), has become the paradigm for how biologists view the social organization of mountain lions, and some other large felids (Smith et al. 1987).

Criteria necessary to invoke social behavior as a mechanism for regulating a population were outlined by Watson and Moss (1970) and emphasized by Seidensticker et al. (1973). Their first two criteria required that reproduction be limited in individuals that could otherwise breed if social interactions with conspecifics did not inhibit them from doing so. The third requirement emphasized that resource limitation must be eliminated as a contributing factor, and that mortality or depressed recruitment attributed to social behavior must be inversely correlated with other causes of mortality or depressed recruitment. Although we do not address the potential for mortality resulting from intraspecific aggression to regulate the population of mountain lions in our study because young mountain lions may have been killed without our knowledge, the

hypothesis of social regulation in mountain lions, however, is generally reliant on a scenario where transient individuals are excluded from becoming permanent members of the population regardless of the availability of prey. Populations of mountain lions are believed to be self-regulating because several studies reported that these large felids remained below the prey-based carrying capacity, suggesting that food was not regulating their populations (Hornocker 1970, Seidensticker et al. 1973, Lindzey et al. 1994). Although mountain lions may partition space and avoid one another temporally, spatial partitioning and mutual avoidance cannot reduce passive competition for resources and therefore, alone, cannot explain population limitation. If social regulation does operate in mountain lions through spatial partitioning of their distributions, then there also must be partitioning of prey. Individuals must exclude conspecifics from enough food to limit reproduction while maintaining more than enough for themselves. This interaction necessarily would occur in areas of distributional overlap, resulting in fewer prey being killed in such areas than would be expected based on resource availability, as Mech (1977) reported for territorial wolves (*Canis lupus*). Furthermore, not only must this prediction hold to invoke social behavior as a mechanism of population regulation, but exclusion from prey also must be demonstrated to explain density limitation of mountain lions through spatial partitioning and mutual avoidance.

The spatial pattern of individuals in a population is the result of adaptive strategies by those individuals ostensibly to maximize reproductive success (Macdonald 1983). For females especially, the patterns observed are often a result of the dispersion

and abundance of food, whereas distributions of males are strongly influenced by the spatial organization of females (Clutton-Brock and Harvey 1978). Understanding the patterns of spatial organization requires information on the arrangement of individuals across the landscape, how they partition space, and the role of sex and age class on such relationships (Kruuk 1995).

For mountain lions to regulate their population or density through a land-tenure system in conjunction with mutual avoidance, the distribution of individuals and their use of prey within an area cannot be random. Individuals must partition space and prey so that each individual has a unique distribution; otherwise, use of food resources would be a result of scramble competition. With such partitioning of food, competition is necessary to account for population regulation.

Gittleman (1989) argued that home ranges that are totally exclusive can develop only where resources are evenly distributed and extremely stable. Each home range must contain adequate food to sustain the individual through the most critical periods while also supplying enough for the remainder of the year. If food resources vary in time and space, an individual may use a region larger than necessary for a particular period of time because resources in that area were necessary at other more-limiting times. This spatial pattern provides opportunities for other conspecifics to make use of the extra space. Such a scenario often leads to a system of overlapping home ranges for solitary carnivores that is a direct result of competition for food resources despite the apparent lack of food limitation (Gittleman 1989). Therefore, distinct distributions of individuals and prey in a

population are necessary to invoke social regulation, but such distributions also can arise in a population regulated by competition.

In addition, if mountain lions were preventing conspecifics from gaining access to prey, we predicted that deer killed by mountain lions would not be randomly distributed, but rather would be clumped within the distribution of individual lions. For social behavior to act as a mechanism allowing mountain lions to sequester prey, individuals should limit the ability of conspecifics to kill prey in that portion of shared distributions. That outcome would result in a nonrandom distribution of kills for the population even if several individuals were so dominant they could use prey within their own distribution at random. A clumped distribution of kills within the distribution of a mountain lion, however, is not evidence of social interactions. A mountain lion distribution may be the result of a variety of needs for that individual resulting in some habitats being used independent of the distribution of prey. Moreover, the behavior of prey alone could cause a clumped distribution of kills within the area used by an individual mountain lion. Therefore, a clumped distribution of deer killed by individual mountain lions within their own distributions would be expected for a population regulated by social behavior but also could be explained by the distribution of habitats or prey. Thus for social regulation to occur, spatial partitioning by mountain lions must be the result of social interactions and not just a function of the distribution of prey. Furthermore, if lion and prey distributions differ, factors other than social behavior, such as different needs and habitat selection, should be considered.

If social interactions between individuals are limiting access to food, then the abundance of prey available to an individual mountain lion in an area shared with another lion should be less than in an area of exclusive use. Even if one individual is dominant in the area of overlap, the result for the population would be fewer prey available in areas of overlapping distributions than in areas of nonoverlap. Finally, if prey are being defended by mountain lions through social interactions to an extent sufficient to limit numbers or density of the lion population, then fewer prey than expected should be killed by mountain lions in areas that they share with conspecifics when compared with areas of exclusive use. Although tests of behavioral regulation of populations have been conducted for a large herbivore (Berger 1986), critical tests of this hypothesis in large carnivores are few.

We tested hypotheses related to how the social organization of the mountain lions might lead to the regulation of their population using an hierarchical approach. We first tested for differences in the spatial distribution of lions within and between the sexes. The absence of spatial differences between individuals would falsify ideas about potential partitioning of prey. We also tested for spatial differences in the distribution of mountain lions and mule deer killed by these predators to assess the potential for competition for food in relation to social organization. Likewise, we examined the clumping of deer kills within the distribution of individual lions to test whether lions might preclude conspecifics from obtaining food. We examined this same relationship for the distribution of lions and live deer. We determined if lions had more deer available within

zones of exclusive use than in areas of overlap. Finally, we tested for differences in the proportion of deer killed in regions of overlap and nonoverlap, controlling for the availability of deer in each area. The failure to find differences in these zones of use would falsify the hypotheses that mountain lions partitioned space to obtain exclusive use of prey. Such sequestering of prey is necessary to posit regulation of the population via social organization.

METHODS

Study area

Round Valley (37°24'N, 118°34'W), located on the east side of the Sierra Nevada in eastern California, is the winter range for a migratory population of mule deer and the mountain lions that prey upon them. The Sierra Nevada casts a rain-shadow over the region to the east of that mountain range. Annual precipitation is highly variable: the coefficient of variation of annual precipitation was 68% during 1951-1987, and precipitation ranged from 3.8 to 45.8 cm (Kucera 1988). Precipitation is strongly seasonal, with about 75% occurring between November and March (Kucera 1988). Temperatures range from -18° C in winter to 37° C in summer.

The predominant vegetation association in Round Valley is typical of the sagebrush (*Artemisia tridentata*) belt described by Storer and Usinger (1968) and is characteristic of the Great Basin. Bitterbrush (*Purshia tridentata*), sagebrush, and rabbitbrush (*Chrysothamnus nauseosum*) predominate in a mosaic where patches of blackbrush (*Coleogyne ramosissima*) and mormon tea (*Ephedra nevadensis*) are

common. *Salix* sp., *Rosa* sp., and *Betula occidentalis* occur in riparian areas. Forbs generally are unavailable in winter, but include *Eriogonum kennedyi*, and *Lomatum* sp. Grasses include *Stipa speciosa*, *Oryzopsis hymenoides*, *Sitanion jubatum*, *S. histrix*, and *Bromus tectorum* (Kucera 1988).

The western edge of Round Valley is bounded by Wheeler Ridge (3,640 m) and Mount Tom (4,161 m), and is characterized by steep, precipitous slopes that are abutted by rocky alluvial fans. Round Valley is bounded to the north by Sherwin Grade at 2,135 m that gently slopes into the valley floor at 1,375 m. The valley extends south, rising into the Buttermilk Country, a region of large boulders and granitic ridges, tall bitterbrush, pinyon pines (*Pinus monophylla*) and Utah junipers (*Juniperus osteosperma*). To the southeast lie the relatively dry and open Tungsten Hills. Highway 395, the main north-south route from Reno, Nevada, to the Los Angeles basin, California, defines the eastern boundary and is coincident with a geological shift into the Volcanic Tablelands. Approximately 3.2 km^2 of this area is developed as residential housing and 18.3 km^2 of open pasture occurs in the lower portion of the valley. Deer do not use these pastures unless heavy snows drive them to lower elevations from areas dominated by bitterbrush. There is one alfalfa ranch, surrounded by a deer-proof fence that is 3-m high. Deer inhabit about 90 km^2 of this range during November-April (Kucera 1988), but the area used varies with snow depth.

The deer herd inhabiting Round Valley migrates to high elevations (> 2500 m) on the west side of the Sierra Nevada (Kucera 1992, Pierce et al. *in press*) to take advantage

of high-quality forage during the dry summer (Kucera 1997). Mule deer accomplish this crossing by moving north or south of the valley and traversing several passes at elevations > 3,000 m. Because of the rain-shadow from the Sierra Nevada, Round Valley is characterized by a much drier climate than the summer range used by deer and mountain lions that migrate to the west side of the crest. These summer ranges are characterized by areas of extensive glaciation with high mountain meadows, Jeffrey pine (*Pinus jeffreyi*), and lodgepole pine (*P. contorta*). Deer remain on the summer range until autumn when winter storms push these herbivores back over the crest and down to the valley floor.

Summer ranges of deer from Round Valley are adjacent to those of deer that winter on the west side of the Sierra Nevada and interspersion of both deer herds occurs (Jordan 1967), as it does between other migratory deer from the west and east sides of that mountain range (Loft et al. 1989). Mountain lions that winter with the west-side herds of deer also move to summer ranges at these higher elevations while following those deer (E. R. Loft *personal communication*, Pierce et al. *in review*). Therefore, two herds of deer share these summer ranges and, consequently, mountain lions from Round Valley repartition space on the winter range after months of being apart. Moreover, these large felids likely interact on the summer range with mountain lions that occupied a separate wintering area.

The deer population wintering in Round Valley declined steadily from about 6,000 (66/km^2) animals in 1985 to < 1,000 (10/km^2) deer in 1991. That decline corresponded with a severe drought and a subsequent reduction in forage availability

(Kucera 1988). The end of the drought coincided with the beginning of our study in 1991. Following the decline of the deer population in the 1980s, estimated numbers of deer on the winter range increased gradually over the period of the study from 1,344 (15/km^2) in 1993 to 1,913 (21/km^2) in 1997. During that same period, average numbers of adult mountain lions located on the winter range by telemetry flights conducted weekly, plummeted from 6.1 in winter 1992-1993 to 3.0 in 1996-1997.

Sampling

We captured 21 adult mountain lions (12 females, 9 males) in Round Valley and fitted them with radio collars from November 1991 to May 1995 using techniques described by Davis et al. (1996). When weather allowed, mountain lions were located weekly via aerial telemetry from a small fixed-wing airplane. We also captured 310 mule deer (217 females, 93 males) and fitted them with radio collars during winter and spring from 1993 to 1997. Deer were captured using Clover traps ($n = 9$; Clover 1956), drop nets ($n = 2$; Conner et al. 1987), and a net gun fired from a helicopter ($n = 299$; Krausman et al. 1985). We captured deer throughout their winter range and intentionally avoided pursuing animals from groups that already included more than one animal that was collared previously. We distributed brown collars among adult males and colored collars among females in the approximate proportion of their estimated occurrence in the population (1:3). Young less than 1 year old ($n = 113$) were fitted with brown, expandable collars close to a 1:1 sex ratio (Bleich and Pierce, *in press*).

Total counts of deer on the winter range in Round Valley have been made

annually in January since 1985 by the California Department of Fish and Game. Counts were conducted by two observers in a helicopter traveling about 75 km/h at an altitude of approximately 60 m. Transects were flown across the valley to the upper elevation at which deer tracks were observed in the snow, and sex and age classes of deer observed were recorded. In 1994 and 1997 snow was not present on the valley floor at the time of the survey, and a modified Lincoln-Petersen method with a "bias adjustment" (Chapman 1951) was used to estimate the deer population. During January male and female deer were in mixed groups and the whole winter range used by both sexes was surveyed so that our estimate was for the entire population. We based this estimate on the number of radio-telemetry collars observed during the count. We used only colored collars that were easily visible from the helicopter; their presence on the study area was confirmed during an aerial-telemetry flight conducted the previous day.

The average number of mountain lions present on the winter range each year was calculated using the number of lions present within the study-area on telemetry flights conducted weekly from November to April. The first year of study was excluded from this analysis because not all lions known to be on the winter range had been fitted with radio collars at that time.

We used a geographic information system (GIS), ARC/INFO (Environmental Systems Research Institute, Redlands, CA), to calculate the distances among individual mountain lions ($n = 21$) for each telemetry flight; accuracy of locations was about 4 ha (Nicholson et al. 1997). We used locations gathered only during flights in winter

(November – March) and only within the boundaries of the study area.

Mule deer killed by mountain lions ($n = 229$) were located by back-tracking lions from day-time positions, investigating mortality signals from radio-collared deer, locating mountain lions at night via radio telemetry, and investigating locations with numerous scavenging birds. The mountain lion responsible for killing a particular deer was positively identified in 179 instances. Of those kills, 112 occurred within the boundary of the study area where we also had data on the distribution of mountain lions and deer between November 1992 and April 1997; only those kills were included in our analyses. Only nine of the deer killed by mountain lions were located using mortality signals from radio collars; therefore, our distribution of kills should not have been strongly biased by our methods of capturing and collaring deer.

We selected 10 radio-collared mule deer at random and visually located them each month during November - April from 1994 to 1997; locations of those deer were estimated using a geographical positioning system accurate to within 40 m. The locations of those live mule deer ($n = 179$) and the locations of kills made by mountain lions were plotted using ArcView 3.0. All methods used in this research were approved by the Institutional Animal Care and Use Committee at the University of Alaska Fairbanks.

Statistical analyses

Analysis of variance (ANOVA) (Zar 1984) was used to test whether distances between pairs of individual mountain lions located during telemetry flights that included

a male ($n = 264$) were different than distances between pairs of individual females with or without young ($n = 472$). We used multi-response permutation procedures (MRPP) including the use of excess groups (Mielke et al. 1983, Zimmerman et al. 1985) to test for spatial differences in the distribution of mountain lions, mule deer, and deer killed by lions (Slauson et al. 1991). We chose this method because MRPP is especially sensitive to distributional changes, even when sample sizes are small (Nicholson et al. 1997). In addition, MRPP evaluates areas used by animals via Cartesian coordinates without estimating the size of home ranges, which can be strongly biased by sample size and autocorrelation of locations (Hundertmark 1997). We report the average within-group distance (the mean distance between all pair-wise locations of an individual) as a descriptive measure of spatial dispersion (Slauson et al. 1991). Because MRPP tests for differences in distributions, we refer to mountain lion and mule deer distributions throughout this paper and avoid using "home range" or "home area" for our results.

We tested for differences in the spatial distributions of 10 mountain lions (8 females, 2 males) using MRPP; the mean number of locations per individual used in our analysis was 26.9 ($SD = 16.5$, Range = 15-70). We tested for an adequate sample size by regressing the average within-group distance for each lion against the number of locations that produced that metric; this relationship was not significant ($r^2 = 0.003$, $P > 0.5$), indicating we obtained an adequate sample size for our analysis. We eliminated 11 adult mountain lions from our analysis because of inadequate sample size. One of those lions was a transient, three had most of their distribution outside Round Valley, several died

after wearing a radio collar for < 1 year, and all had too few telemetry locations in Round Valley during winter. Locations of the remaining 10 lions from the winters of 1992 - 1997 were combined. Most of these lions were not present during all study years, and this population of mountain lions was not closed during the 5 winters of our study. Eliminating 11 mountain lions increased the likelihood that we would find clumping in the spatial distribution of the remaining 10 lions, whereas combining winters during which not all lions were present had the opposite bias. This elimination of some mountain lions had no effect on analysis of use of prey between individuals. Our inference, then, is based on resident lions having most of their winter distribution in Round Valley and that survived long enough for collection of a sufficient number of locations within the study area.

The MRPP model used Universal Transverse Mercator coordinates (meters) (Northings and Eastings) as response (dependent) variables and individual lions (1-10) as the main effect (the grouping variable). We did not perform a multivariate shape correction because the response variables were measured in the same units (meters). We also used MRPP to ask whether there was a difference in the overall distribution of lions ($n = 269$) and our sample of mule deer located on the ground ($n = 179$). Locations of deer were pooled across winters (1995 - 1997) because MRPP indicated those locations were not different spatially ($P > 0.125$).

The MRPP also was used to analyze the overall spatial distribution of deer and the kills made by lions. In addition, we used MRPP to ask if the kills made by a particular

lion were clumped within its spatial distribution. We performed this latter test for each individual; we used the chi-square method of Sokal and Rohlf (1981) for combining probabilities from independent tests to obtain overall comparisons for male and female mountain lions.

We also tested whether deer were more abundant in areas where distributions of mountain lions overlapped as opposed to areas of exclusive use. We partitioned data such that a pair of mountain lions with an overlap in their distributions were on the study area at the same time ($n = 24$ pairs). We used a sign test (Zar 1984) to ask if proportionally more deer occurred in areas where distributions of mountain lions overlapped or in areas of exclusivity for individuals. We treated pairs with nonconcordant outcomes (i.e., one animal with more deer in its exclusive area but the other with more deer in the zone of overlap) as ties.

Finally, we examined the effect of conspecifics on the distribution of kills made by a particular mountain lion. We determined the expected value for kills by calculating the proportion (i.e., abundance) of live mule deer from our random sample, that occurred within zones of overlap for pairs of lions and for areas where the spatial distributions of pairs did not overlap. The same spatial approach was followed for kills made by the respective lions. We then summed expected kills and observed kills for all comparisons involving a pair of lions. This pair-wise approach, however, artificially inflated sample size because the kills made by one lion could be counted more than once in several pairings. Consequently, we used these data to proportionalize the actual kills ($n = 107$)

into zones of overlap and nonoverlap, and then performed a chi-square analysis (Zar 1984) based on actual kills. We repeated this analysis for female mountain lions alone (pairs = 15, kills = 92). These tests revealed if there was an effect of a distributional overlap among lions on where deer were killed while simultaneously controlling for the distribution of deer.

RESULTS

The spatial distribution of 10 mountain lions varied significantly across Round Valley (MRPP, $P < 0.0001$). The within-group distance of individuals averaged 5,754 m (SD = 1,958 m). This relationship held when distributions for the eight females (MRPP, $P < 0.0001$) and two males (MRPP, $P < 0.003$) were considered separately; within-group distances averaged 4,326 m (SD = 2,835) for females and 7,788 m (range = 5,763-9,813 m) for males. Although overlap occurred in the locations of individual mountain lions (Fig. 2.1.), significant clumping in distribution occurred for both sexes, with females exhibiting generally shorter within-group distances than males. The distance between pairs of individual mountain lions also differed by social category (Fig. 2.2). Pairs containing males were significantly ($F_{1,734} = 11.02$, $P < 0.001$) farther apart than pairs among social categories of females.

The distribution of mule deer killed by the 10 mountain lions differed significantly across the study area (MRPP, $P < 0.0001$). Within-group distances for kills ($\overline{X}$ = 4,355 m, SD = 2,279 m) generally were less than those between locations of

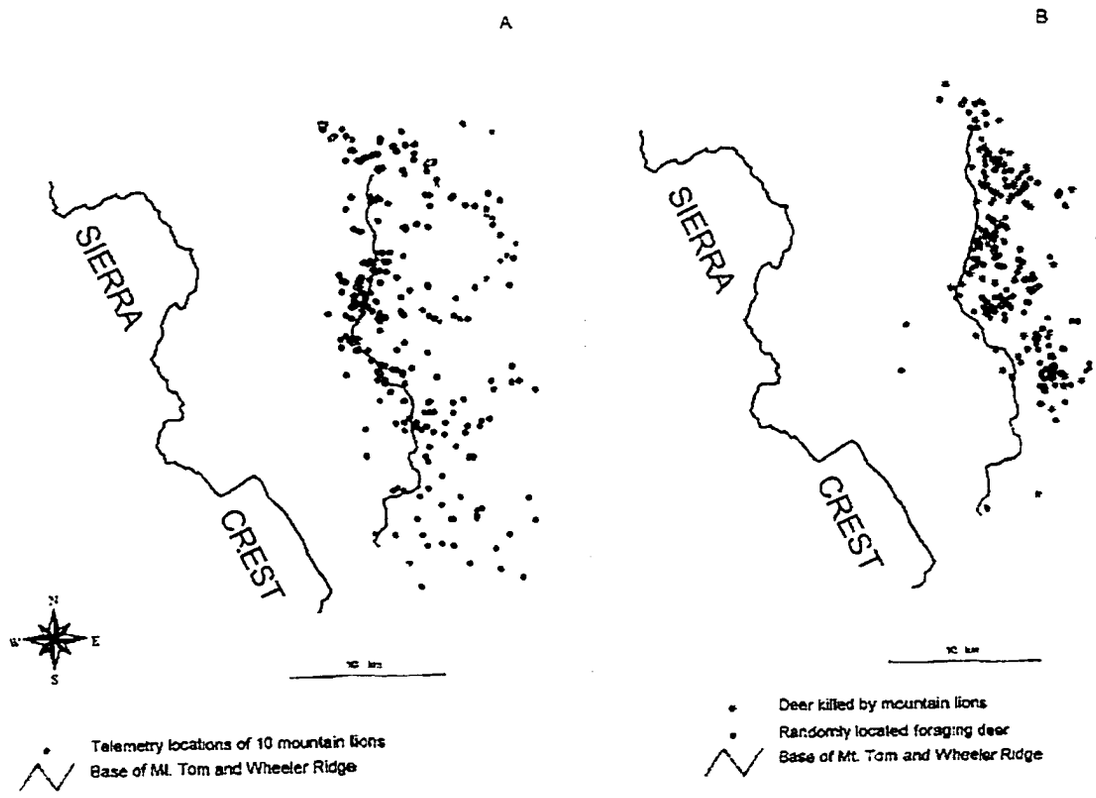

FIG 2.1. A) Radio-telemetry locations of 10 mountain lions on the Round Valley, California, winter range of mule deer in 1992-1997. B) Locations of radio-collared deer, which were randomly selected and visually located, and deer killed by 10 mountain lions, on the Round Valley winter range, 1992-1997.

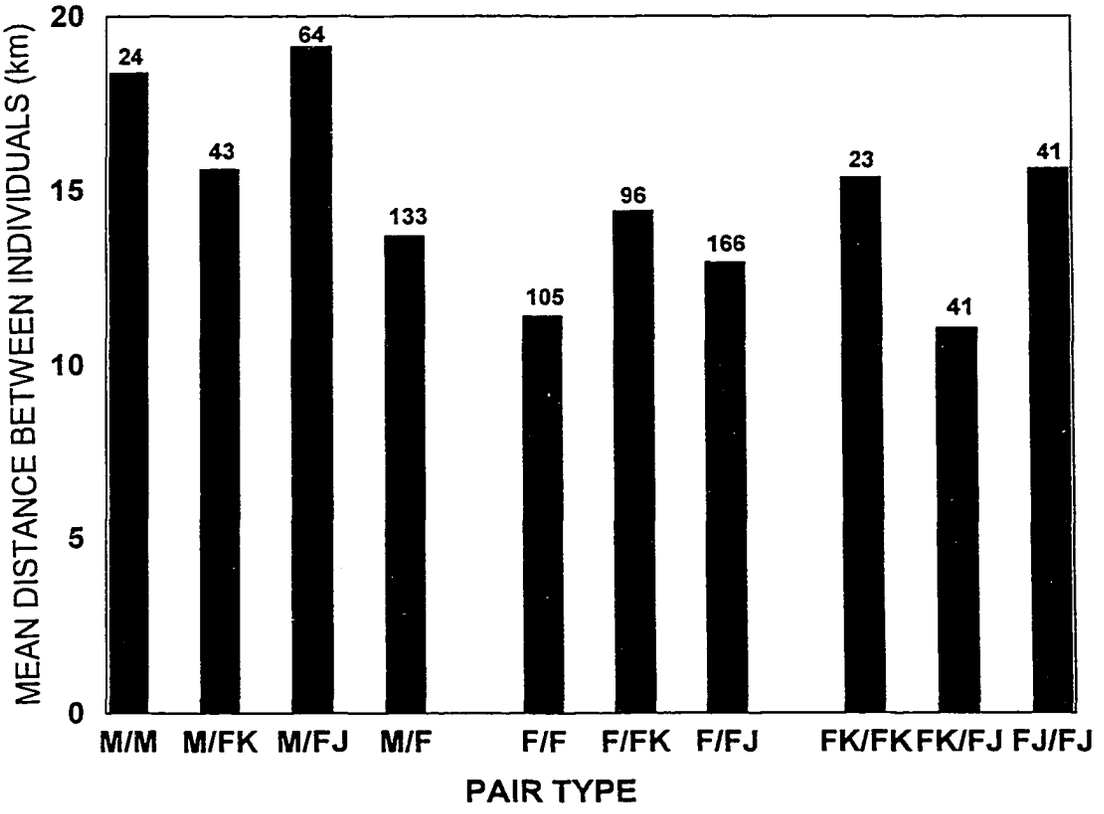

FIG. 2.2. Mean distances between individual adult mountain lions of different social categories in Round Valley, California, winter 1992-1997. Distances were calculated for each radiotelemetry flight; M = Male, F = Female, FK = Female with kitten(s), FJ = Female with juvenile(s). Average distance between pairs of individuals that included males was significantly larger than those that did not include a male. Sample size of pairs is given above bars.

mountain lions.

We further examined the distribution of kills with respect to the locations of the lion that made them using MRPP. Four of eight females showed a clumping of kills within their distribution ($P < 0.05$), whereas neither male did so ($P > 0.20$). The overall pattern, however, was for kills to be clumped within the distribution of a lion. This pattern held when we combined probabilities from the tests for all 10 lions ($X^2 = 49.8$, 20 *df*, $P < 0.005$) or for the eight females ($X^2 = 46.4$, 16 *df*, $P < 0.005$), but not for the two males ($X^2 = 5.0$, 4 *df*, $P > 0.25$). This general clumping of kills within the distributions of lions may have resulted from lions including steep, rugged terrain along Wheeler Ridge and Mt. Tom in their distributions; deer were less plentiful in these steep areas than on the alluvial fans of Round Valley (Fig. 2.1). Consequently, we compared the distributions of deer with those of lions. As expected from the previous analysis, the distribution of predators and their primary prey differed significantly (MRPP, $P < 0.002$). We then asked whether this outcome was a result of lions using areas where deer were uncommon by making deer the excess group in our analysis. This test indicated ($P > 0.9$) that the locations of lions could have been obtained in a random draw from the joint distributions of both deer and lions, meaning that the difference obtained in the previous analysis was not a result of deer being outside the distribution of mountain lions, but that mountain lions were using some areas where deer were uncommon. Thus, if we excluded those steep rugged areas seldom used by deer, the locations of deer likely determined the distribution of lions.

We also compared the locations of live mule deer with those of kills made by mountain lions; the outcome of this test was marginally not significant (MRPP, $P = 0.061$). By making deer the excess group, we further tested whether kills could have been obtained from a random draw from the joint distributions of kills and deer; the answer was yes ($P = 0.83$).

We also tested whether the distribution of deer was related to the manner in which lions partitioned space. This test was restricted to 24 pairs of lions that were on the study area at the same time. We asked if proportionally more deer locations occurred within zones of exclusivity or overlap within the distributions of the paired lions. Overall, 15 pairs of lions had more deer in zones of overlap than in exclusive areas, three pairs had more in zones of exclusivity, and six pairs were scored as ties. A sign test indicated that this pattern was highly significant ($P = 0.003$).

Finally, we compared the expected distribution of kills (based on the proportional occurrence of live deer in zones of lion exclusivity and overlap) with the observed distribution of kills. The expected distribution for kills was over two-fold higher in the zones of overlap between lions than in areas of exclusivity; the proportion of observed kills in these zones was nearly identical to what was expected (Fig. 2.3). This pattern also held when we partitioned these data for parings involving only females ($X^2 = 0.162$ $P > 0.50$); sample size was too small to perform this analysis for males only. Proportionally fewer deer occurred in areas of exclusive use by mountain lions than in zones of overlap, and this distribution of deer, rather than the spatial organization of lions (i.e., partitioning

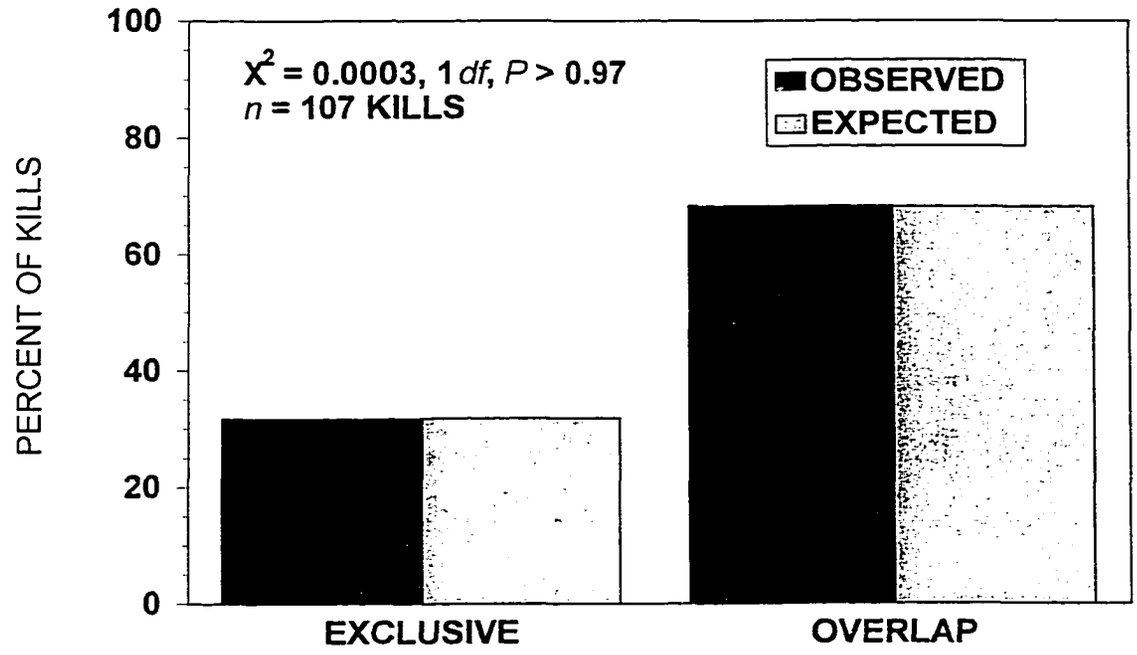

FIG. 2.3. Expected and observed number of mule deer killed by pairs of mountain lions for regions where the distributions of those individuals in a pair overlapped and for regions of exclusive use by each individual in the pair, Round Valley, California, winter 1992-1997. Expected values are based on the proportion of live mule deer located in each region.

of prey resource) was largely responsible for where kills occurred.

Discussion

The social system of mountain lions has been the focus of several investigations (Seidensticker et al. 1973, Padley 1990, Sweanor 1990, Beier et al. 1995). Relatively few studies on the ecology of mountain lions, however, have examined in depth the spatial relationships of lions with their primary prey. Pierce et al. (*in press*) described long-range movements of mountain lions as they followed the migration of mule deer over the crest of the Sierra Nevada in California. Although seasonal shifts in the home ranges of mountain lions following their prey have been observed previously (Seidensticker et al. 1973, Hemker et al. 1984, Anderson et al. 1992), those shifts did not require most individuals within a population to interact with conspecifics unfamiliar to them, because individuals within a population moved together. The mountain lions that migrated across the crest of the Sierra Nevada had to reestablish themselves in areas occupied by mountain lions they had not encountered for > 6 months. This migratory behavior may have affected the social system of mountain lions because social organization can vary within species as a result of differences in the distribution or movements of food (Lott 1984). This phenomenon of varying social organization has been observed among other large felids (Schaller 1972). Furthermore, migratory movements make the maintenance of exclusive areas of use more difficult (Schaller 1972, Caro 1994), and variation in the timing or distribution of food increases the likelihood of overlapping distributions of individuals in a predator population (Gittleman 1989).

Indeed, variation in carnivore social organization is related to the availability of prey (Litvaitis et al. 1986, Packer 1986, Moehlman 1989). The migratory behavior of mountain lions raised questions about the role of spatial partitioning and mutual avoidance in the use of food among individuals. As a result, we tested several hypotheses related to the social system of mountain lions and how it was associated with distribution of prey, and evaluated results of those tests in light of the potential for that social system to intrinsically regulate populations of mountain lions.

Mountain lions in Round Valley have a dynamic social system that includes extensive overlap of distributions in winter, and long-range movements in association with migrating mule deer in spring and autumn (Pierce et al. *in press*). A system of overlapping home ranges has been described for most populations of mountain lions, with the distribution of females overlapping each other more than overlap among males, but with males having larger home ranges that encompass those of several females (Hornocker 1969, Logan et al. 1986, Cunningham et al. 1995). Our examination of individual distance measures, which included a temporal component, also indicated that males had a broader spatial arrangement than did females, and were spaced further from other conspecifics than were females (Fig. 2.2). That result was consistent with previous findings that male mountain lions move greater distances than females and have larger home ranges (Anderson et al. 1992, Beier et al. 1995); similar findings have been reported for another large, solitary felid (Mizutani 1993). Despite the common use of space in Round Valley, we observed a significant difference in the distribution of

individual mountain lions on their winter range. This clumping of individuals occurred for both males and females, but was more pronounced among females.

The distribution of deer killed by mountain lions also was clumped within the distributions of individual lions, as was the distribution of live deer. When we controlled for the use of cliffs around Mt. Tom and Wheeler Ridge by mountain lions, however, the distribution of mountain lions was not different than that of live deer; the clumping of deer kills within distributions of mountain lions likely resulted from lions using areas during the day where deer were not plentiful (i.e., Wheeler Ridge and the slopes of Mt. Tom) (Fig. 2.1). Such a pattern of lion distributions could result from a distribution of food that varied in time or space (Gittleman 1989), and that may not be dependant on social interactions. Results we observed, however, also could have occurred if mountain lions were excluding one another from access to prey. Thus, social behavior might be involved in determining how mountain lions partitioned space, and resource partitioning might be occurring. The potential for population regulation or density regulation based on spatial partitioning and mutual avoidance was not falsified by these analyses.

Deer kills could be explained primarily by the distribution of live deer within the distributions of mountain lions. This result, however, was marginally not significant, and indicated that where mountain lions killed deer within the boundaries of their own distributions may have been influenced by other ecological factors. Vulnerability, habitat selection, or other factors may affect where predators kill prey (Bertram 1973, Sunquist and Sunquist 1989, Pierce et al. 1992, Stander and Albon 1993). For instance, Bowyer

(1987) reported that group size of mule deer affected the outcomes of interactions between deer and their predators. Moreover, size and composition of ungulate social groups change throughout the year, as do patterns of habitat selection by these large herbivores (Bowyer 1984, 1986, Bleich et al. 1997, Bowyer et al. 1998); all of these variables could affect where deer were killed. Indeed, Bleich (1999) reported that terrain strongly affected the outcome of predator-prey encounters.

In addition, we predicted that if mountain lions were sequestering prey (i.e., preventing use by conspecifics) by partitioning space, the distribution of live deer would reflect this behavior and we would find fewer deer than expected in areas shared by a pair of mountain lions than in regions of exclusive use by these lions. Our results, however indicated the opposite (Fig. 2.3). Significantly more mule deer occurred in areas of overlap than in areas of exclusive use. Mountain lions were using areas based on the availability of deer, not based on the presence of conspecifics. Our finding that most deer occurred in areas used by multiple mountain lions indicates that the distribution of deer, rather than social interactions, explained how mountain lions used space. Those results, however, do not preclude the possibility that individual lions were preventing conspecifics from killing prey in areas of overlap and sequestering more deer for themselves in shared areas. Further analysis revealed that prey killed by each mountain lion also could be explained by the distribution of deer alone. Pair-wise comparisons of mountain lions using common areas did not demonstrate an effect of potential social interactions on the use of prey. Thus, the greater abundance of deer in areas where

distributions of mountain lions overlapped was not the result of deer seeking regions of lower predation pressure, as suggested for deer subjected to predation by wolves (Mech 1977). Indeed, the high degree of overlap in the distribution of lions (Fig. 2.1) indicates that these regions of overlap were not boundary areas of limited use by lions, and thus would not allow deer to avoid lions by using such areas. Concomitantly, the lack of sequestering of prey by mountain lions in regions of overlapping distributions eliminates the only mechanism available to limit a population or its density through spatial partitioning and mutual avoidance, unless mortalities of mountain lions were caused by intraspecific aggression.

Seidensticker et al. (1973) emphasized that the difference between "density regulation" and "population regulation" was important but often confused. Those authors explained that density may be limited in a defined area because individuals were prevented from establishing residency in that area; however, if those same individuals became breeding members elsewhere, the "population" had not been limited. Nonetheless, in the absence of mortality caused by intraspecific aggression, the regulation of a population or its density must be the result of limited reproduction and, therefore, directly related to the availability or vulnerability of resources (Berger 1986). For regulation to be the result of social behavior and not simply competition, individuals must exclude conspecifics from food in a manner sufficient to limit reproduction while maintaining more food than they need for themselves to maximize reproduction. Furthermore, temporal avoidance does not reduce passive competition for resources and

does not lead to exclusive availability of food.

For social behavior to be implicated as a mechanism of population regulation, food resources must be excluded as a limiting factor (Watson and Moss 1970). Therefore, for the land-tenure system proposed for mountain lions, individuals should have exclusive territories that encompass more prey than necessary for maximum reproduction. Our data do not support this hypothesis; mountain lions did not make exclusive use of prey, and we observed no indication of a land-tenure system that would lead to regulation of the population.

Intraspecific aggression in mountain lions can lead to death, and defense of prey can be risky (Anderson et al. 1992, Bleich et al. 1996, Pierce et al. 1998). Therefore, spiteful behavior (Ricklefs 1990) must be invoked to explain why animals sequester more food than is necessary for maximum reproduction. A scenario where selection for such potentially costly behavior could evolve without the direct benefit of increased fitness is difficult to imagine. Behavior that increases fitness through maximum reproduction cannot be invoked as a mechanism for social regulation of a population.

Hemker et al. (1984) reported a decline in a population of mountain lions in Utah with a decrease in deer numbers, and concluded that the density of the predator ultimately was controlled by prey abundance. Similarly, during the course of our study, the average number of adult mountain lions on the winter range declined sharply following the crash of the mule deer population. This decline undoubtedly was more pronounced than reported herein because nine adult lions were present in Round Valley during winter

1991-1992, of which four died and one disappeared prior to November 1992 . We did not include this first winter of study in our population estimate because we did not have all known mountain lions collared and available to be monitored from the airplane until that summer. The pattern observed in our study is typical of that described for many single predator-single prey systems where there is a time lag in the crash of the predator population following the decline of its prey (Elton 1924, Utida 1957, Finerty 1980, O'Donoghue et al. 1998). Such changes in numbers of mountain lions and mule deer are consistent with the hypothesis that density of this felid in Round Valley also was controlled by abundance of prey.

The social system of mountain lions in Round Valley during winter included individuals that spaced themselves apart (Fig. 2.2), but had extensive overlap in their distributions determined largely by the location of prey. Partitioning of space occurred most extensively in areas where prey was not abundant, whereas areas of overlap had more than two-fold the number of deer available to mountain lions (Fig. 2.3). In the region where prey were available within the distribution of a mountain lion, the distribution of kills was not affected by social organization. The distribution of deer killed by mountain lions could be explained solely by the distribution of the deer population. Mountain lions in Round Valley most likely were limited by prey availability and not social behavior. Whether our conclusion will hold for nonmigratory populations or populations with much higher densities of prey is uncertain, and deserves further study. We note, however, that there is a paucity of research simultaneously examining the

distribution of predators and their prey (Kruuk 1995). Our study was the first critical test of the effects of prey distribution on the partitioning of food by mountain lions. We clearly demonstrated that neither sequestering of prey nor a land-tenure system occurred, and social organization could not be invoked to explain the dynamics of the mountain lion population. The pattern of social organization in mountain lions we observed may be more wide spread than previously thought, and more research on both these large predators and their prey under varying conditions is needed to thoroughly test this hypothesis. We further suggest our study has implications for understanding the predator-prey dynamics in other large mammals.

ACKNOWLEDGMENTS

We thank the houndsmen and field technicians that helped capture and radio-track mountain lions, including J. Davis and V. Davis, J. Ostergard, C. Baker, C.-L. B. Chetkiewicz, G. Raygorodetsky, and D. Stoner. Many thanks to members of the Air Services branch of the California Department of Fish and Game, particularly R. Anthes. Help from C. Howard and M. Nicholson with GIS was greatly appreciated. We also thank J. Wehausen for help capturing mountain lions. This work could not have been accomplished without the help of volunteers, W. Allsup, G. Clarkson, H. Jones, R. Noles, D. Noles, N. Partridge, P. Partridge, B. Peters, P. Thompson, and the late R. Williamson. D. Person, E. Rexstad, and J. Kie helped with statistical analyses and E. Rexstad, V. Van Ballenberghe, and R. G. White provided useful comments on the manuscript. Many thanks to K. Mayer, E. Loft, S. Mastrup, and R. Mohr for their support and administrative

assistance. This research was supported by the California Department of Fish and Game (CDFG), The National Rifle Association, The Mule Deer Foundation, Friends of the National Rifle Association, Safari Club International, the California Deer Association, the Fish and Game Advisory Committee of Inyo and Mono counties, University of California White Mountain Research Station, and the Institute of Arctic Biology at the University of Alaska Fairbanks. This is a contribution from the California Department of Fish and Game Deer Herd Management Plan Implementation Program, and is Professional Paper 010 from the Eastern Sierra Center for Applied Population Ecology.

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[3]CHAPTER 3.

HABITAT SELECTION BY MULE DEER: FORAGE OR RISK OF PREDATION BY MOUNTAIN LIONS?

Abstract: We conducted research in the eastern Sierra Nevada, California, USA, from 1994 to 1997. Stands of bitterbrush (*Purshia tridentata*) in the Great Basin provided relatively greater cover for mule deer (*Odocoileus hemionus*) than surrounding patches of rabbitbrush (*Chrysothamnus nauseosum*) or desert peach (*Prunus andersonii*). Bitterbrush is critical forage for mule deer during winter. Consequently, mule deer that overwinter in the Great Basin may be confronted with a tradeoff between forage benefits and predation risks with respect to habitat selection. Thus we tested for habitat selection by mule deer on their winter range. We hypothesized that mountain lions (*Puma concolor*), which stalk and ambush prey, would be more successful at killing mule deer in habitat with more concealment cover. Logistic regression indicated that mule deer selected habitat at greater elevations ($P < 0.001$) with more bitterbrush ($P < 0.001$) and less rabbitbrush ($P = 0.033$) than at random locations. Logistic regression also indicated that mountain lions killed deer in relatively open areas with more desert peach ($P < 0.001$) than locations in which deer foraged. Therefore, deer were not confronted with a

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[3] Pierce, B. M., R. T. Bowyer, and V. C. Bleich. In review. The role of mountain lions in shaping habitat selection by mule deer. *Journal of Wildlife Research.*

tradeoff in terms of habitat selection on winter range and minimized the ratio of predation risk:forage by selecting habitat with more bitterbrush. These results have important conservation implications because they suggest that mountain lion predation does not indirectly affect reproduction by limiting access to high quality forage for mule deer on the winter range. We hypothesize that changes in diet among seasons, which occur for herds of migratory deer, lead to individuals experiencing changing predation risk:forage ratios throughout the year. Hence, migratory populations of mule deer likely adopt different strategies of habitat selection among seasons.

Key-words: forage, Great Basin desert, *Odocoileus hemionus*, predation, *Puma concolor*.

INTRODUCTION

Selection of habitats to maximize reproductive fitness can involve a tradeoff between maximizing foraging benefits while minimizing risk of predation (Berger 1991, Longland 1994, Molvar and Bowyer 1994, Bleich et al. 1997, Nicholson et al., Kie 1997). This tradeoff has been proposed for a number of systems (Sih 1980, Pierce et al. 1992, Sweitzer et al. 1996, Rachlow and Bowyer 1998), but only can occur if foraging benefits and predation risk are positively related (Bowyer et al. 1998). An understanding of how forage and risk of predation vary across the landscape and how those factors are interrelated is necessary for understanding habitat selection (Bleich et al. 1997). Most

research examining habitat selection of ungulates has focused on resource acquisition; however, more recent studies have emphasized the importance of avoiding predators while acquiring those resources (Van Ballenberghe and Ballard 1994, Sinclair and Arcese 1995, Bowyer et al. 1998, Bleich 1999). Few studies have examined the manner in which risk of predation and forage are arrayed in natural environments, or have tested for the effects of such landscape heterogeneity on actual outcomes from encounters between large carnivores and their primary prey.

Because habitat selection in herbivores likely affects reproductive fitness, strategies of habitat selection can be linked to the dynamics of their populations. Differences in age class and sex can play an important role in habitat selection (Clutton-Brock 1991, Bleich et al. 1997). For example, young of mule deer (*Odocoileus hemionus*), young have very different habitat requirements than adults (Bowyer 1986, Loft et al. 1987); however, the location of young may be the result of foraging needs of their mothers (Bowyer et al. 1998). Bleich et al. (1997) noted that male bighorn sheep (*Ovis canadensis*) responded more to foraging needs, whereas habitat selection by females was affected more by the risk of predation. For this reason, examining differences in use of habitats between the sexes of ungulates is critical before evaluating risk of predation.

We studied habitat selection of mule deer in relation to predation by mountain lions (*Puma concolor*) on a winter range in the eastern Sierra Nevada, a major mountain range in California, U.S.A. Predators that stalk and ambush prey, like mountain lions, are

thought to prefer areas with greater hiding cover for hunting (Schaller 1972, Russell 1978, Beier et al. 1995). Indeed, mountain lions were more successful at hunting pronghorn (*Antilocapra americana*) that inhabited rugged terrain with more vegetation than those that occurred in open prairie (Ockenfels 1994). The primary forage of mule deer on our study area was bitterbrush (*Purshia tridentata*) (Kucera 1997), which often grows to >2 m in height and, in general, provides more hiding cover than surrounding patches dominated by other shrubs. We hypothesized that stands of bitterbrush would provide ideal habitat for mountain lions engaged in hunting and, because of the importance of bitterbrush as forage, we predicted that there would be a positive relationship between predation risk and foraging benefit. Under such a scenario, reproduction by mule deer could be indirectly affected because mountain lion predation could limit access to high quality forage on the winter range, as it does for some populations of mountain sheep (Wehausen 1996). Mule deer would have to make a tradeoff, selecting habitat that minimizes the risk of predation while maximizing foraging opportunities.

If risk of predation by mountain lions is constant across habitats occupied by mule deer, or if mountain lions are more successful at killing deer in habitats with low foraging benefits, there would be no tradeoff available for mule deer when selecting habitat in which to forage. Under such circumstances, mule deer should seek to maximize foraging benefits without regard to predation risk from mountain lions. If, however, mountain lions are more effective hunters in areas with stalking cover, then a more complex

strategy of habitat selection would be required of deer. We examined the role of forage availability and predation risk by mountain lions in the selection of habitat by mule deer. We tested the null hypotheses that mule deer foraged randomly throughout the habitats available on our study area, and that risk of predation by mountain lions upon mule deer was constant across those habitats. We also tested for differences between male and female mule deer in use of habitat during winter.

For habitat selection by mule deer to be affected by mountain lions, those carnivores must be a significant predator on mule deer in our system as they are in neighboring regions of the Great Basin (Bleich and Taylor 1998). Hence, we compared the proportion of mortality in mule deer by mountain lions with that of mortality by other predators. We predicted that there would be a positive relationship between amount of bitterbrush (e.g., forage) and stalking cover (e.g., predation risk) and, consequently, the potential for tradeoffs to be made by mule deer when selecting habitat in which to forage. Having detailed knowledge of both the locations at which deer foraged and the locations in which mountain lions preyed upon deer allowed us to determine those parameters most important for selection of habitat by these two large mammals and to determine the strategy for habitat use by mule deer.

We thank the houndsmen and others that helped capture mountain lions and locate deer killed by mountain lions, including J. Davis, J. Ostergard, W. Allsup, C. Baker, C.-L. Chetkiewicz, P. Partridge, G. Raygorodetsky, D. Stoner, and J. Wehausen. We extend our gratitude to the volunteers who monitored mule deer, G. Clarkson, H. Jones, R.

Noles, D. Noles, N. Partridge, P. Partridge, B. Peters, P. Thompson, and the late R. Williamson. Special thanks are extended to V. Davis, who did most of the habitat sampling. We also thank J. A. K. Maier for help with GIS analyses. This research was supported by the California Department of Fish and Game (CDF&G), University of California White Mountain Research Station, The National Rifle Association, Friends of the National Rifle Association, The Mule Deer Foundation, Safari Club International (Los Angeles, Orange County, Sacramento, San Fernando, and San Francisco Bay Area chapters), the Fish and Game Advisory Committee of Inyo and Mono Counties, and the Institute of Arctic Biology at the University of Alaska Fairbanks. This is a contribution from the CDF&G Deer Herd Management Plan Implementation Program and is Professional Paper 013 from the Eastern Sierra Center for Applied Population Ecology.

STUDY AREA AND METHODS

Round Valley (37°24'N, 118°34'W) is located on the east side of the Sierra Nevada in eastern California, USA. Mount Tom (4,161 m) and Wheeler Ridge (3,640 m) form a steep boundary along the western edge of Round Valley with rocky alluvial fans spreading eastward from their bases. The valley floor at 1,375 m gently rises northward to the top of Sherwin Grade at 2,135 m. The south end of the valley is composed of large boulders and granitic ridges, tall bitterbrush, pinyon pines (*Pinus monophylla*) and Utah junipers (*Juniperus osteosperma*). The Tungsten Hills provide relatively dry and open habitat in the southeastern portion of the study area. The eastern boundary of Round

Valley is delineated by Highway 395, the main north-south route from Reno, Nevada, to the Los Angeles basin, California, which is coincident with a geological shift into the Volcanic Tablelands. Approximately 18.3 km^2 of open pasture occurs in the eastern portion of the valley and 3.2 km^2 of the study area is developed as residential housing. Deer did not use those pastures unless heavy snows drove them to lower elevations from areas dominated by bitterbrush. Deer inhabited about 90 km^2 of that range during November-April (Kucera 1988), but the area used varied with snow depth.

The vegetation association in Round Valley is characteristic of the Great Basin and typical for the sagebrush belt (Storer and Usinger 1968). Winter range is composed of bitterbrush, sagebrush (*Artemisia tridentata*), and rabbitbrush (*Chrysothamnus nauseosum*) in a mosaic where patches dominated by blackbrush (*Coleogyne ramosissima*), desert peach (*Prunus andersonii*) and Mormon tea (*Ephedra nevadensis*) are common. Riparian areas support the growth of *Salix* sp., *Rosa* sp., and *Betula occidentalis,* but forbs and graminoids are uncommon in Round Valley during winter.

In June 1995, a fire burned approximately 22 km^2 of winter range near the center of our study area. This fire occurred in habitat composed predominately of bitterbrush and sagebrush. The fire was of sufficient enough intensity that no measurable regrowth of bitterbrush occurred from the charred stumps. In the years following the fire, desert peach and cheat grass (*Bromus tectorum*) dominated vegetative growth, and provided little cover for deer or mountain lions.

During the late 1980s, forage availability in Round Valley, as indexed by leader

growth of bitterbrush, declined sharply in response to a prolonged drought (Kucera 1988). A decline in the population of mule deer, from about 6,000 (66/km^2) animals in 1985 to < 1,000 (10/km^2) deer in 1991, coincided with the decrease in carrying capacity of the winter range. Our study began in November 1991, coincident with the end of that drought. Estimated numbers of deer on the winter range increased gradually over the period of the study from 1,344 (15/km^2) in 1993 to 1,913 (21/km^2) in 1997, while the density of mountain lions decreased sharply during that same period. The average number of adult mountain lions located on the winter range during telemetry flights conducted weekly, plummeted from 6.1 in winter 1992-1993 to 3.0 in 1996-1997 (Pierce et al. *in press*).

Sampling

Three-hundred and ten mule deer (217 females, 93 males) were captured in Round Valley and fitted with radiocollars during winter or spring from 1993 to 1997. Deer were captured using Clover traps (n = 9; Clover 1956), drop nets (n = 2; Conner et al. 1987), and a net gun fired from a helicopter (n = 299; Krausman et al. 1985). Deer were captured throughout their winter range and animals in groups that already included more than one animal that was collared previously were intentionally avoided. Brown collars were distributed among adult males and colored collars among females in the approximate proportion of their estimated occurrence in the population (1:3). Young, <1 year old (n = 113), were fitted with brown, expandable collars close to a 1:1 sex ratio (Bleich and Pierce *in press*). Twenty-one adult mountain lions (12 females, 9 males) also

were captured and fitted with radiocollars from November 1991 to May 1995, using techniques described by Davis et al. (1996). All aspects of this research were approved by the Institutional Animal Care and Use Committee at the University of Alaska Fairbanks.

Mule deer killed by mountain lions ($n = 229$) were located by back-tracking lions from day-time positions, investigating mortality signals from radiocollared deer, locating mountain lions at night via radio telemetry, and investigating locations at which numerous birds were observed scavenging. The location where deer were killed was determined by back-tracking drag-marks. Drag-marks are made in the ground by deer carcasses when the mountain lions drag deer after making a kill. Evidence of broken brush, tracks and blood also were used to confirm the location where deer were killed by mountain lions. Only instances that occurred from November through April 1994-1997, within the boundaries of the study area, and for which the location where the deer was killed could be identified ($n = 41$) were used in our analyses. All collared deer were monitored daily for mortality signals and causes of mortality were determined by examining wounds, tracks, and feces in the vicinity of the carcass; predator identification often was confirmed with the use of remote photography (Pierce et al. 1998). Ten mule deer fitted with radio collars were selected at random by their VHF frequency, and located visually during daylight hours each month from November through April 1994-1997. In addition, 10 random locations were selected each month during that same period. Our radiocollared sample of mule deer was random, therefore, the group sizes

individuals occurred in should have been representative of what was available for mountain lions. We were not able to examine the effect of group size on predation by mountain lions, however, because we could not determine the group size that deer killed by mountain lions occurred in. Young deer were still with their mothers on the winter range and therefore our random sample should not have been biased by habitat differences between young and adult deer.

At all locations of deer killed by mountain lions, locations of live deer, and random sites, a 50-m tape was oriented in a random direction and the line-intercept method (Canfield 1941) was used to sample cover of shrubs. The total distance along the tape of each plant species intersected was determined and six species, (bitterbrush, sagebrush, rabbitbrush, desert peach, Mormon tea, and blackbrush) composed $\geq$ 5% each of the total vegetation measured. Proportion of random locations that had each of the six species present (bitterbrush 44%, sagebrush 55%, rabbitbrush 41%, Mormon tea 43%, blackbrush 33%, desert peach 23%) suggested that all species types were sufficiently available to provide a choice for mule deer. An arcsin-square root transformation was performed on the proportion that each of those six species composed of the 50-m measurement at each location. A 2-m cover pole (Griffith and Youtie 1988) divided into eight equal sections was viewed from the four cardinal directions at a distance of 15 m. The total number of sections that were >50% obstructed from view from each direction was recorded as an index to concealment cover. Samples of bitterbrush from plants within a 50-m radius of the location being characterized were collected. Samples taken

from bitterbrush were about 10 cm in length and included more than current annual growth: those samples were typical of leaders removed by foraging deer on this heavily browsed winter range. All samples were stored in paper bags and desiccated quickly in the dry desert air. Moisture content for bitterbrush was calculated for all samples collected during 1996-1997 by subtracting total weight after drying from original weight. In-vitro dry matter digestibility (IVDMD) and percent nitrogen (N) were determined for all samples collected using standard techniques (Van Soest 1982) at the Nutrition Laboratory, University of Alaska Fairbanks.

Fecal pellets of mule deer were collected throughout the study area during November-April. Each month, 10 samples composed of $\geq$10 pellets were collected from the northern and southern halves of the study area. Only fresh ($\leq$1 day old) pellets were collected and five pellets from each sample were grouped into composite samples each month. Microhistological identification of plant fragments (Sparks and Malechek 1968) was completed for composite samples by the Composition Analysis Laboratory, Fort Collins, Colorado, USA.

The Geographic Information System (GIS) Arc/Info (Environmental Systems Research Institute, Redlands, CA, USA) was used to derive several variables including elevation, slope, distance to the nearest paved road and distance to the nearest riparian zone. The viewshed was determined as the number of pixels (900 m^2 units) that could be seen from a deer with its head at a height of 1 m to a maximum of distance of 400 m. An index of terrain ruggedness was determined by multiplying the angular deviation of

aspect by the *SD* of slope (Nicholson et al. 1997) for a radius of 210 m.

Statistical analyses

Step-wise logistic regression (Agresti 1990) ($\propto$ to enter and stay = 0.15) was used to test for differences in habitat selection between male and female mule deer on the winter range. That same method also was used to determine the variables most influential in predicting the locations of deer from random locations, and the locations of deer killed by mountain lions from locations of foraging deer. Multicollinearity was controlled for by eliminating any variables with $r^2 \geq 0.5$; 13 variables considered biologically relevant were available for inclusion in the regressions. The final model was based on the approximate chi-squared distribution of the reduction in deviance achieved by adding variables (McCullagh and Nelder 1989). Hosmer-Lemeshow goodness-of-fit tests were used to assure the aptness of the models. Multivariate analysis of variance (MANOVA) was used to test for differences in forage quality (IVDMD, N) and moisture content of bitterbrush among location types (Neter et al. 1990).

We used chi-square analysis (Zar 1984) to test for differences in the proportion of mule deer killed by mountain lions (n = 41), coyotes (*Canis latrans*)(n = 17) and bobcats (*Lynx rufus*)(n = 2) between January 1993 and April 1998. Only mule deer wearing radio telemetry collars were used for this analysis to eliminate bias in our ability to locate deer that died from these different sources of predation. Linear regression (Neter et al. 1990) was used to examine the relationship between the value from our coverpole and the

percent cover of bitterbrush to test for the potential for a tradeoff between predation risk and forage availability. We used SAS (SAS Institute 1998) or SPSS (Norusis 1993) statistical packages for analyses of data.

RESULTS

Predation by mountain lions composed 68% of predator-caused mortality among mule deer, whereas predation by coyotes and bobcats constituted 28% and 4% of mortality on collared deer, respectively. Mountain lions were the primary predator on mule deer in our study ($X^2 = 37.8$, $df = 2$, $P < 0.001$).

Logistic regression indicated that adult male and female deer did not use habitat differently in Round Valley during winter ($P > 0.15$); therefore, data for males and females were pooled. Young were still traveling with their mothers and, hence, were included with adult females for analysis. Although linear regression of cover with bitterbrush did not produce a highly predictive model, the results indicated a highly significant relationship ($r^2 = 0.061$, $P < 0.001$) in a positive direction. Consequently, the potential for a tradeoff by mule deer between predation risk and forage benefit existed. Such a tradeoff was contingent, however, on a situation where predation risk was greater in habitat with more cover, and habitat composed mostly of bitterbrush provided the best forage.

A significant logistic model was produced that distinguished locations of mule deer from random locations:

Pr (deer locations) = 4.0954 + 0.0450(cover) + 3.789(bitterbrush) -

2.0963(rabbitbrush) - 0.00288(elevation); $P = 0.0001$.

This outcome indicated that mule deer did not occur equally across available habitats, but instead selected areas with more bitterbrush ($P = 0.0003$) and less rabbitbrush ($P = 0.033$), and that were at lower elevations ($P = 0.0001$) (Fig. 3.1). Although concealment cover was not significant ($P = 0.08$), its inclusion significantly improved the ability of the model to categorize deer locations from random ones. Concordance of the final model for habitat selection by mule deer was 70%, and the Hosmer and Lemeshow goodness-of-fit statistic indicated that the model was apt ($X^2 = 11.72$, d.f. = 8, $P = 0.16$).

The habitat in which mountain lions were successful at killing mule deer also differed from the habitat in which deer most frequently occurred. The resulting model for habitat where mountain lions killed deer was:

Pr (lion kills) = -4.2098 + 2.3635(rabbitbrush) + 3.1229(desert peach) +

0.00138(elevation); $P = 0.0019$.

Mountain lions were able to capture prey in habitat that was more likely to have desert peach ($P = 0.002$) than areas where deer occurred (Fig. 3.2). Elevation ($P = 0.09$) and rabbitbrush ($P = 0.07$) also significantly improved the ability of the model to distinguish locations where deer were killed by mountain lions from the locations in which deer foraged. Concordance of the overall model for locations where deer were killed by mountain lions was 66% and the Hosmer Lemeshow goodness-of-fit statistic indicated the model was apt ($X^2 = 6.405$, d.f. = 8, $P = 0.60$).

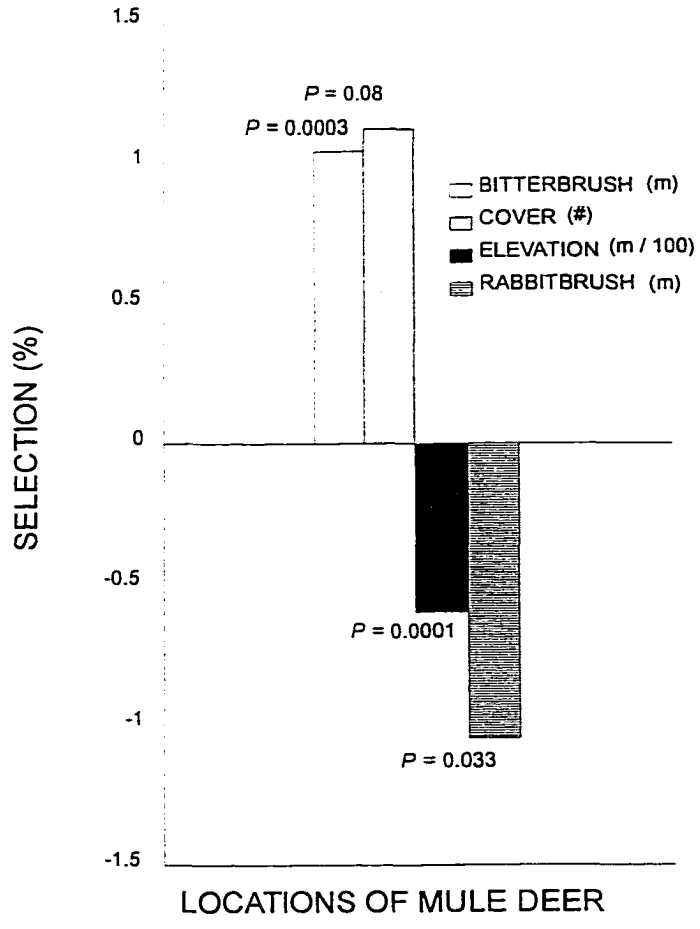

Fig. 3.1. Selection (used minus available) of habitat by mule deer in the Great Basin, California, USA, from 1994 to 1997. Step-wise logistic regression indicated mule deer selected (use > availability) habitat with more bitterbrush and greater concealment cover, which were at lower elevations, but avoided (use < availability) habitat with an abundance of rabbitbrush.

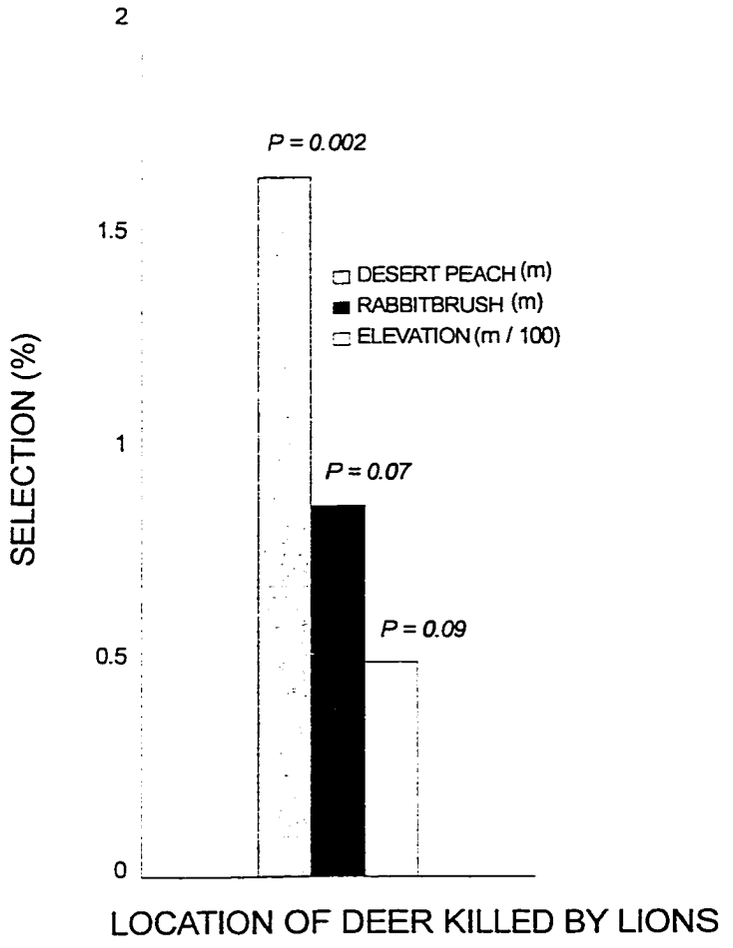

Fig. 3.2. Selection (used minus available) of habitat in which mountain lions killed mule deer in the Great basin, California, USA, from 1994 to 1997. Step-wise logistic regression indicated mountain lions selected (use > availablility) habitat to kill deer with more desert peach and rabbitbrush at greater elevations than locations in which deer chose to forage.

Microhistological analyses of fecal pellets collected from mule deer confirmed that bitterbrush was their primary forage on winter range (Fig. 3.3). Although the proportion of sagebrush increased in the diet of mule deer throughout the winter, bitterbrush averaged >65% of their diet during November - April. Analyses of bitterbrush indicated that moisture content (%)($F_{2,89} = 1.53$, $P = 0.22$) and nitrogen (%) ($F_{2,222} = 1.97$, $P = 0.14$) did not vary among random locations (33% $\pm$ 10.7 SD; 1.4% $\pm$ .21 SD), deer locations (34% $\pm$ 13.7 SD; 1.4% $\pm$ .27 SD), or locations of lion-killed deer (40% $\pm$ 6.6 SD; 1.4% $\pm$ .17 SD); there was no difference in forage digestibility between random locations (50% $\pm$ 8.0 SD) and those selected by deer (48% $\pm$ 9.0 SD)(Tukey's, $P > 0.05$). Mule deer, however, were killed by mountain lions in areas where the digestibility of bitterbrush was lower (42% $\pm$ 8.0 SD) than locations where deer foraged, and locations of random sites within the study area (Tukey's, $P < 0.05$).

DISCUSSION

Our data are unique in understanding habitat selection by large herbivores because no one has investigated how deer select habitat while simultaneously examining sites where herbivores perished from predation. Previous studies of habitat use by mountain lions have described them as preferring areas with woody vegetation, and having moderate to extreme terrain ruggedness that provided cover for hunting (Hornocker 1970, Seidensticker et al. 1973, Dixon 1982). We examined the factors that might influence habitat selection by mule deer and predation by mountain lions. Because mountain lions

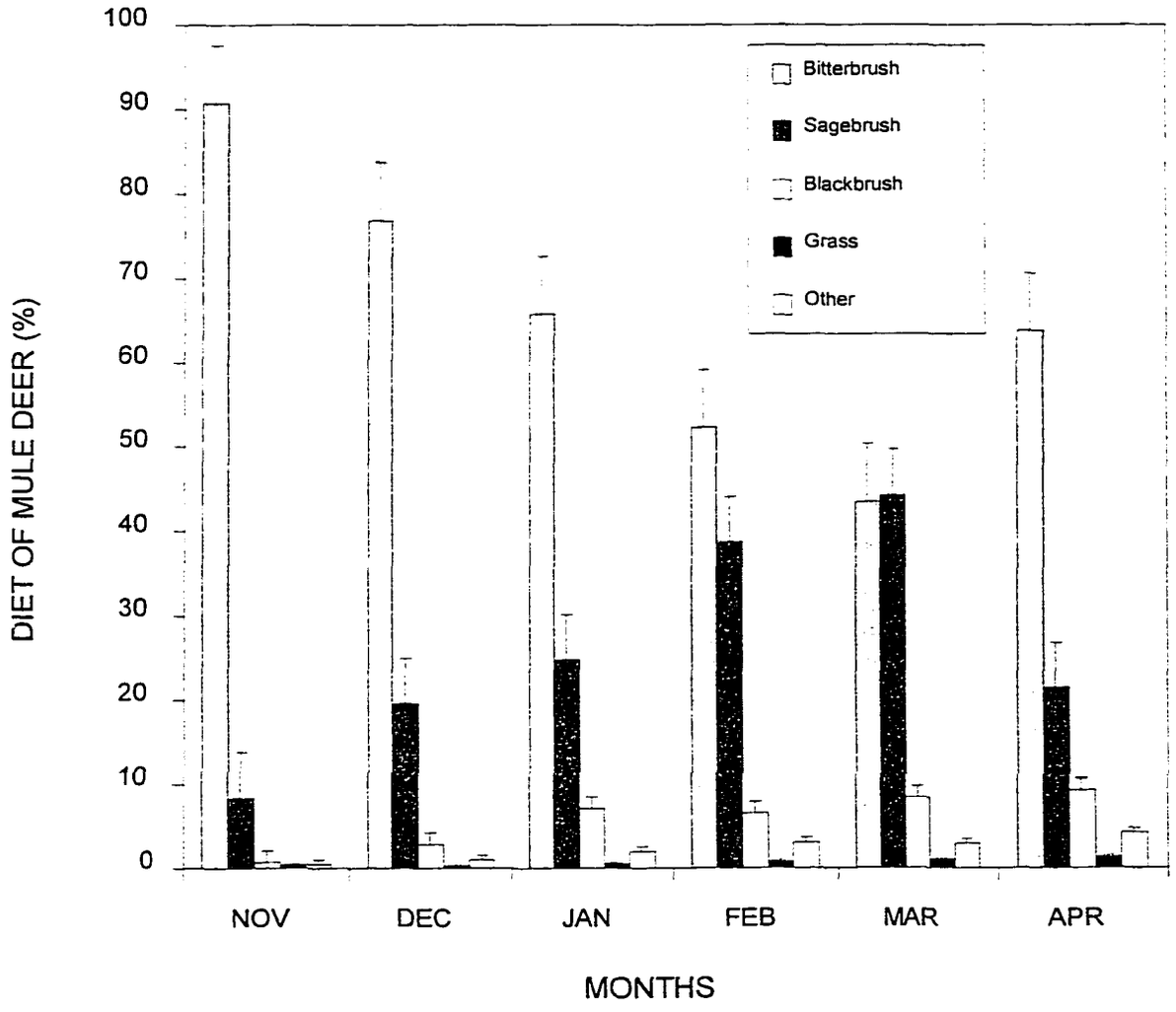

Fig. 3.3. Diet composition of mule deer on a winter range in the Great Basin, California, USA, from 1992 to 1997.

stalk and rush prey (Koford 1946), habitat that provides some hiding cover may be necessary for successful capture of prey as suggested for African lions (*Panthera leo*)(Schaller 1972) and mountain lions killing pronghorn (Ockenfels 1994). Consequently, we hypothesized that such areas might pose more risk to mule deer in terms of the potential for being preyed upon. Although we did not have data on attempts made by mountain lions to kill deer among different habitat types, we assumed that the number of mule deer killed in a particular habitat reflected the risk associated with foraging there for an individual. Contrary to our prediction based on the literature, bitterbrush and cover did not enhance the likelihood of a mountain lion killing a deer in our study area. That contradiction may be a result of other studies using daytime locations that encompassed the general habitat used by mountain lions, and that did not focus on hunting locations or the effects of the distribution of prey. Indeed, mountain lions are nocturnal and hunt and feed primarily at night (Beier et al. 1995, Pierce et al. 1998). These solitary felids may select areas for resting during the day that are very different from the type of habitat in which they hunt. Deer in Round Valley appeared most active during dawn and dusk, but also could be observed foraging throughout the day. A lack of distinct activity peaks is not uncommon for mule deer during winter (Dusek 1975). Furthermore, individual deer in Round Valley were repeatedly located in the same area on a daily basis. Although we were unable to document locations of randomly selected deer during the night, data collected from locations of daytime foraging on winter range likely were representative of foraging locations of deer while

mountain lions were actively hunting.

Mountain lions in our study area posed the most significant threat of mortality to mule deer from a predator. If mule deer selected habitat in response to levels of predation risk, then predation by mountain lions should play an important role in habitat selection for mule deer. Furthermore, selective pressure from mountain lions could differ between males and females; however, we observed no significant difference in habitat selection between the sexes of mule deer during winter. Sexual segregation at parturition is common in *Odocoileus* (McCullough et al. 1989, Bowyer 1984, Bowyer et al. 1996), but not all populations segregate in winter (Bowyer 1984). Results from our study indicated that for mule deer on the winter range, differences in the risk of predation between sexes did not affect selection of habitat.

Our results confirmed that bitterbrush could provide significant concealment cover on the winter range for deer. Bitterbrush has been identified as the preferred forage for deer on this range (Kucera 1997; Fig. 3.3.) and is considered an important species for wintering mule deer in other areas (Wallmo 1981). Sagebrush was the second most common forage in the mule deer diet however, average digestibility of bitterbrush from Round Valley (51%) was considerably higher than reported for dormant *Artemisia tridentata* (39%) in other studies (Crampton and Harris 1956). Therefore, a positive relationship between forage benifit and stalking cover could exist provided that predation risk increased with bitterbrush cover.

Mule deer selected habitats that had a relatively high proportion of bitterbrush and

low proportion of rabbitbrush. These locations tended to be at lower elevations and had more concealment cover than random ones. These results indicated that if mountain lions were more successful at killing deer in areas with substantial concealment cover, then mule deer would be making a tradeoff: accepting more risk for greater foraging benefits. This hypothesis, however, was rejected. Mountain lions killed more deer in habitat with desert peach and rabbitbrush, two low-lying shrubs associated with more open terrain than at locations where foraging deer occurred.

We suggest that for mule deer to minimize predation risk from mountain lions in the Great Basin, these herbivores should attempt to forage in areas with concealment cover nearby, particularly stands of bitterbrush. Such a strategy does not require a tradeoff if bitterbrush is the best available forage. Thus, mule deer wintering in the Great Basin or similar regions should seek to minimize their predation:forage ratio (Pulliam 1989) by remaining in habitat with a high proportion of bitterbrush.

Although the locations where mule deer eventually were killed by mountain lions were in more open areas than where deer foraged, our data indicate that deer killed by mountain lions may not have been foraging in open habitat when a pursuit began. Our analyses included only locations where individual deer were killed and did not include information on where deer were located before encountering the mountain lion or where the carcass eventually was cached. That outcome also could explain why forage quality was lower at locations where deer were killed by mountain lions. Samples of bitterbrush taken from these more open areas, with a greater amount of desert peach and rabbitbrush,

may represent bitterbrush plants growing under less than ideal conditions. Deer killed in those more-open habitats may not have chosen to forage there and might have fled there during pursuits. Mountain lions may be more successful at catching deer that flee into relatively open areas than individuals that flee into areas with a number of obstacles. If so, selecting areas with vegetative and rock cover would be adventageous for deer, suggesting that mountain lions should attempt to drive deer into more open terrain when in pursuit.

If deer that fled into open areas when pursued by mountain lions were more likely to be caught than deer that stayed in habitat with more cover, then habitats that border open areas may be more risky in terms of mountain lion predation than more densely vegetated areas away from edges. In Great Basin habitats, edges between stands of bitterbrush and open areas of desert peach and rabbitbrush probably do not provide the added forage diversity that exists along meadow edges or in early successional woodlands.

A strategy of selecting stands of bitterbrush with substantial concealment cover also may be the best way for mule deer to minimize risk from other predators. Stotting behavior, which occurs in mule deer but not white-tailed deer (*Odocoileus virginianus*), may be an adaptive behavior for eluding predators in habitats with numerous obstacles (Lingle 1992). Additionally, risk of predation by coyotes may be less in areas with substantial cover. Bleich (1999) noted that mortality from coyote predation for bighorn sheep was proportionally greater in open terrain than in more rugged terrain, and Bowyer

(1985) reported that group size increased significantly for mule deer as they moved > 30 m from cover, suggesting that deer sensed greater risk of predation in more open areas. Moreover, Bowyer (1987) reported that mule deer were as apt to flee from coyotes as to stand their ground, and Bleich (1999) suggested that proximity to cover was an important factor in the outcome of such encounters. Studies of other canids suggest that they often pursue prey for relatively long distances (Mech 1966, Estes and Goddard 1967) in which open terrain might be an advantage to predators by allowing the more vulnerable members of a herd to be identified.

We emphasize that our results were dependant on a situation where cover was correlated with availability of high-quality food. Many populations of mule deer are migratory, including our study population (Kucera 1992, Pierce et al. *in press*). Forage quality and availability change dramatically with season for deer in Round Valley (Kucera 1997). During periods when the diet of mule deer was composed predominantly of forbs and graminoids, strategies involving a tradeoff between predation risk and forage benefits may indeed prevail. Hence, for prey species that migrate seasonally or alter diet use across seasons, habitat selection may reflect a broad spectrum of tradeoffs.

Our results indicate that cover still may be a necessary component of the habitat where mountain lions stalked mule deer, but that mountain lions were more likely to capture and kill deer in habitat that is more open than where deer normally occurred. For that reason, mule deer in Round Valley do not have to make a tradeoff between foraging benefit and predation risk when selecting habitat. For our system, mule deer can

minimize their predation risk:forage ratio by selecting habitat with a high proportion of bitterbrush that is away from the open terrain associated with desert peach or recent wildfires. Consequently, mountain lion predation does not appear to limit access to high quality habitat for mule deer, on the winter range, in Round Valley.

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[4]CHAPTER 4.

Prey selection by mountain lions and coyotes: effects of hunting style, body size, and reproductive status

Predation on mule deer (*Odocoileus hemionus*) by mountain lions (*Puma concolor*) and coyotes (*Canis latrans*) was examined to test the effects of hunting style, body size and, for mountain lions, reproductive status on selection of prey by these large carnivores. Mountain lions, which hunt by stalking, selected (use > available) young mule deer (≤ 1 year old) as prey. Body condition of mule deer did not affect prey selection by coyotes or mountain lions ($P = 0.47$), and both predators selected females ($P < 0.05$) and older adult deer ($P < 0.001$). Mountain lions consumed more mule deer, whereas the diet of coyotes was composed primarily of small animals ($P < 0.05$). Body size of mountain lions may have affected the sex of prey selected by these large felids. Female mountain lions selected female deer more so than did male lions ($P < 0.05$). Female mountain lions without offspring, however, did not differ from male mountain lions in prey selection ($P = 0.18$), and coyotes did not select for young deer ($P = 0.42$). Female mountain lions with kittens were highly selective for young deer in late summer ($P < 0.01$). Reproductive condition of mountain lions was an important factor driving prey selection.

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[4] Pierce, B. M., V. C. Bleich, and R. T. Bowyer. In review. Prey selection by mountain lions and coyotes: effects of hunting style, body size, and reproductive status. *Oikos*.

Differences in age, sex, and physical condition may predispose segments of an ungulate population to predation, and cause important changes in the demography and dynamics of the prey (Curio 1976, Taylor 1984). These factors also may vary with the size of predator or the method of hunting (e.g., stalking verses coursing; Bleich 1999). Ungulate populations are subject to predation by both canids and felids, and these predators often vary in body size and style of hunting (Schaller 1967, 1972, Mech 1970, Packer et al. 1990, Huggard 1993, Karanth and Sunquist 1995). Furthermore, anti-predator strategies of prey may vary with group size, age, sex, and habitat use of prey (Bowyer 1987, Bleich 1999). Most ungulates are sexually dimorphic with males significantly larger than females (Ralls 1977, Weckerly 1998), and males often possess horn-like structures (Lincoln 1992) that can increase the risk of injury to a predator (Hornocker 1970). Differences in morphology among sex and age classes of ungulates can result in varying risk associated with predation and lead to variation in selection of prey. Finally, the physical condition of prey can affect their ability to escape predation, and predators may kill animals in poor condition preferentially because selection for more vulnerable prey requires less energy and poses less risk (Mech 1970). Mountain lions (*Puma concolor*) and coyotes (*Canis latrans*) which prey on mule deer (*Odocoileus hemionus*) provide an opportunity to compare selection of ungulate prey by predators that differ substantially in body size and hunting style.

Coursing predators such as wolves (*Canis lupus*) may pursue moose (*Alces alces*) for long distances (Mech 1970), assessing the condition of the moose and the likelihood

of successfully killing them (Peterson 1977). Wild dogs (*Lycaon pictus*) also pursue prey over great distances (Estes and Goddard 1967) and Kruuk (1972) noted that spotted hyenas (*Crocuta crocuta*) were more successful at killing prey if the chase was > 300 m. In contrast, most felids are stalking predators (Ewer 1973, Leyhausen 1979) that rely on cover and stealth (Seidensticker 1976, Sunquist 1981) to approach prey closely and then rush and pursue an individual over a relatively short distance (Elliott et al. 1977, Van Orsdol 1984). This form of ambush hunting has been reported for mountain lions (Beier et al. 1995). When prey occur in groups (Bowyer 1984, 1987), as it does for mountain lions preying on mule deer, the stalking technique of felids could limit their ability to select for young, old or weakened animals (Schaller 1972). Consequently, we predicted that coyotes, a coursing predator, would be more likely than mountain lions, a stalking predator, to select mule deer in poor physical condition or from vulnerable age classes. In addition, we predicted that male and female mountain lions would not differ in their selection of prey unless other factors, besides hunting style, were important determinants of prey selection.

Body size also may influence prey selection in carnivores (Bekoff et al. 1984). Predation on large ungulates can be risky and result in injury or death of a predator (Packer 1986, Mech 1970). Injuries to mountain lions from attacking prey are well documented (Gashwiler and Robinette 1957, Hornocker 1970, Brown et al. 1988, Ross et al. 1995). Most felids are solitary hunters and tend to kill species weighing more than one-half their own body weight (Gittleman 1985, Packer 1986). Because male mountain

lions can be > 50% larger in body size than females (Dixon 1982), sexual dimorphism may lead to differences between males and females in risk associated with killing prey. Indeed, Ross and Jalkotzy (1996) reported differences in prey selection by male and female mountain lions: males were significantly more likely to kill moose, whereas females avoided killing moose and selected deer. Furthermore, predators may select young animals because they are less skillful at escape (Curio 1976, Vitale 1989). Consequently, if body size affects prey selection, then smaller predators should exhibit greater selection for small prey. We predicted that coyotes would kill a greater proportion of young deer than would mountain lions, and that female mountain lions would kill a greater proportion of young deer than would males. Among adult deer, we predicted that coyotes would kill a greater proportion of female deer than would mountain lions, and female mountain lions would kill a greater proportion of female deer than would male mountain lions.

Finally, prey selection may vary among social categories within a predator species as a result of differences in behavior or energetic needs. Male and female mountain lions may encounter different sex and age classes of deer at varying frequencies because of differences in habitat selection, timing and amount of movement, or size of home-range of these large predators. The energetic needs of male and female mountain lions likely vary because of differences in body size or the demands of rearing young. We tested the hypothesis that social categories of mountain lions would kill mule deer differentially with respect to sex and age classes of deer, and specifically whether reproductive

demands of females affected prey selection.

Methods

Study Area

Round Valley (37°24'N, 118°34'W) is located on the east side of the Sierra Nevada in eastern California, USA. The eastern boundary of Round Valley is delineated by Highway 395, the main north-south route from Reno, Nevada, to the Los Angeles basin, California, USA, and is coincident with a geological shift into the Volcanic Tablelands. Deer inhabited about 90 km^2 of that range during November-April (Kucera 1988), but the area of use varied with snow depth. Most mule deer that spend winter in Round Valley migrate in spring to high-elevation summer ranges in the Sierra Nevada (Kucera 1992, Pierce et al. *in press*). A small proportion of the herd, however, remained on the eastern side of the mountains and were prey for resident mountain lions and coyotes throughout the year.

The vegetation in Round Valley is characteristic of the Great Basin and typical for the sagebrush (*Artemisia tridentata*) belt (Storer and Usinger 1968). Bitterbrush (*Purshia tridentata*), sagebrush, and rabbitbrush (*Chrysothamnus nauseosum*) predominate in a mosaic where patches of blackbrush (*Coleogyne ramosissima*) and mormon tea (*Ephedra nevadensis*) are common. *Salix* spp., *Rosa* spp., and *Betula occidentalis* occur in riparian areas. Detailed descriptions of the study area are provided by Kucera (1992) and Pierce et

al. *(in press)*.

Temperatures in Round Valley range from -18° C in winter to 37° C in summer; annual precipitation is highly variable and ranged from 3.8 to 45.8 cm (Kucera 1988). Precipitation is strongly seasonal, with about 75% occurring between November and March (Kucera 1988).

Our study began in November 1991 and coincided with the end of a prolonged drought. Estimated numbers of deer on the winter range increased gradually over the period of the study from 1,344 (15/km^2) in 1993 to 1,913 (21/km^2) in 1997, whereas the mean number of mountain lions decreased markedly, from 6.1 in winter 1992-1993 to 3.0 in 1996-1997 (Pierce *et al. in review*).

Sampling

Three-hundred and ten mule deer (217 females, 93 males) were captured in Round Valley and fitted with radio collars during winter or spring from 1993 to 1997. The radio collars were programed to emit a mortality signal if the collar remained motionless for > 6 hrs. Deer were captured using Clover traps (n = 9; Clover 1956), drop nets (n = 2; Conner et al. 1987), and a net gun fired from a helicopter (n = 299; Krausman et al. 1985). Each year deer were captured throughout the winter range and individuals from groups that already included more than one animal that was collared previously were intentionally avoided. Collars were distributed among adult males and females in the approximate proportion of their occurrence in the population (1:3). Young (<1 year old; n = 113)

were fitted with collars close to a 1:1 sex ratio (Bleich and Pierce, *in press*). Twenty-one adult mountain lions (12 females, 9 males) and 21 offspring (< 1 year old; 14 male, 7 female) were captured from November 1991 to May 1996 using hounds (Davis et al. 1996) or foot snares. We weighed mountain lions, to the nearest 2.5 kg, using a spring scale, and mean weight of adult mountain lions was determined using the first recorded weight for each individual (males, $n = 8$; females, $n = 11$). All adults were fitted with radio-telemetry collars. Nine kittens (≤ 6 months old) from three litters were captured in natal dens (Bleich et al. 1996). Age of young mountain lions was estimated using weight, pelage characteristics, and patterns of tooth eruption (Ashman et al. 1983, Anderson 1983). All methods used in this research were approved by an Institutional Animal Care and Use Committee at the University of Alaska Fairbanks.

Helicopter surveys were conducted annually in January to determine the proportion of adult male, adult female, and young mule deer on the winter range. Aerial transects were flown with three observers and extended across the entire study area to an elevation at which deer tracks in snow no longer could be seen.

Mule deer killed by mountain lions ($n = 229$) and coyotes ($n = 57$), during 1991-1998, were located by back-tracking lions from day-time positions, investigating mortality signals from radio-collared deer, locating mountain lions at night via radio telemetry, and investigating locations with numerous scavenging birds. All collared deer were monitored daily for mortality signals, and causes of mortality were determined by examining wounds and tracks, and feces in the vicinity of carcasses. Predators

responsible for a kill often were confirmed with the use of remote photography (Pierce *et al.* 1998). Lower incisors and femurs were collected from all carcasses of mule deer for age analysis using cementum annuli (Low and Cowan 1963), and analysis of fat in the marrow of long-bones (Neiland 1970), respectively.

Feces of carnivores were collected opportunistically (mountain lion, $n = 261$; coyote, $n = 253$) for analysis of diets. Identification of food in fecal samples was determined from remains of bone, teeth, claws, and hair samples examined for color, length, thickness and medullary characteristics (Big Sky Laboratory Florence, MT). Remains identified from carnivore feces were categorized as mule deer, small animals (< 15 kg), or other, and were summarized as percent occurrence in feces (Bowyer et al. 1983).

We used deer killed by automobiles, during 1991-1998, to estimate sex, age class, and physical condition of prey available to predators. Use of such animals as a random sample of a population has been questioned (O'Gara and Harris, 1988) because deer in poor condition may be more likely to use roadways for paths of travel through deep snow. This potential problem, however, was not a consideration for our study area. Most deer (55% of 191 deer) killed by automobiles were collected from Highway 395, and snow depth rarely was greater than a few centimeters in the vicinity of that roadway. Highway 395 is a major four-lane highway with considerable traffic at all hours, and deer killed along the roadway were not there to avoid deep snow. To ensure our sample of deer killed by automobiles was not biased, we tested for differences in age composition of

those deer against data obtained from aerial surveys.

In addition to using deer killed by automobiles as a random sample to test for prey selection, we also estimated proportion of "postnatal deer" (< 4 months old) in the population during late summer (July-September) using fetal rates. Adult females were collected randomly from the deer population annually in March following the methods of Kucera (1997). The mean number of fetuses per adult female (n = 86) from 1992 to 1996 was used to estimate the proportion of postnatal deer in the population in late summer. The use of fetal rates to estimate the available proportion of postnatal deer available in late summer does not account for mortality and therefore is an overestimate. Thus, our estimate of selection for postnatal deer by predators was extremely conservative.

Data analysis

We compared the proportion of "young deer" (< 1 year old) killed by automobiles in late summer with the proportion of postnatal deer (< 4 months old) expected (51%), based on fetal rates of adult females collected in March. That analysis indicated that young deer were underestimated in road kills during late summer; therefore, we used only data from October-June to test for prey selection by mountain lions and coyotes. For comparisons in which age category was controlled (e.g., sex and age of adults), data from throughout the year were used because these data were not biased by the birthing season of mule deer.

Analysis of variance (ANOVA) was used to test for differences in the age (in

years) of adult deer killed by automobiles, mountain lions, and coyotes throughout the year, and to test for differences in the percent fat in the marrow of adult females killed by vehicles in March of 1993 and 1994 ($n = 6$) and the adult females collected in March of the same years ($n = 31$). We used multi-dimensional chi-square analysis (Zar 1984) to determine if there were differences in categories of age, sex, and condition of mule deer killed by automobiles, mountain lions, and coyotes from October-June. Mule deer were categorized as young (< 1 year) or adult, and good condition (> 50% fat in bone marrow) or poor to meet assumptions of chi-square analysis. The use of bone marrow fat to index condition may be problematical because these fat deposits are the last to be used by ungulates (Mech and DelGuidice 1985); therefore an animal that has used most of its body fat reserves and is in poor condition may still have some fat in the marrow of their long bones. Although we collected several other measures of body condition for deer killed by automobiles, including kidney fat and heart fat, deer killed by mountain lions and coyotes rarely provided these data because these organs often were consumed. When bone marrow fat in red deer (*Cervus elaphus*) reaches ca. 50%, kidney fat values approach ca. 25% (Riney 1955). Low kidney fat values coincide with other indices of malnutrition, therefore, our results assume that deer with $\leq 50\%$ bone marrow fat were in poorer condition than those with > 50%. We tested for differences in categories of age, sex, and condition of mule deer, from all months, killed by automobiles and different social categories of mountain lions. Social categories of mountain lions included solitary adult males, solitary adult females, adult females with juveniles (> 6 months old but not

independent) and adult females with kittens ($\leq$ 6 months old; Pierce et al. 1998).

Because female mountain lions gave birth to litters in late summer (Bleich et al. 1996), females with young consistently had a higher proportion of young deer available as prey when compared with other social categories. For that reason, we partitioned our data to test for prey selection by female mountain lions with kittens. Using chi-square analysis, we compared the proportion of postnatal deer killed by female mountain lions with kittens (61%), with proportion of postnatal deer in the population during late summer (51%) estimated from fetal rates.

Results

Analysis of prey remains in carnivore feces indicated that mule deer were the primary food of mountain lions, whereas the remains of mule deer occurred in a significantly smaller percentage of coyote feces (Fig. 4.1). Desert cottontails (*Sylvilagus audubonii*) and black-tailed jack rabbits (*Lepus californicus*) composed the primary species of small animals in the diet of both mountain lions and coyotes (Fig. 4.1).

Chi-square analysis of the mean ($\pm$ SD) proportion of young in the population determined by aerial surveys (26% $\pm$ 4.4) and the proportion killed by automobiles (25% $\pm$ 8.4) between October-April, from 1993 to 1998, did not differ significantly with years pooled ($X^2 = 0.158$, df = 1, $P = 0.69$) or within any year ($P \geq 0.19$). Thus, mule deer killed by automobiles reflected the proportion of young deer in the population on

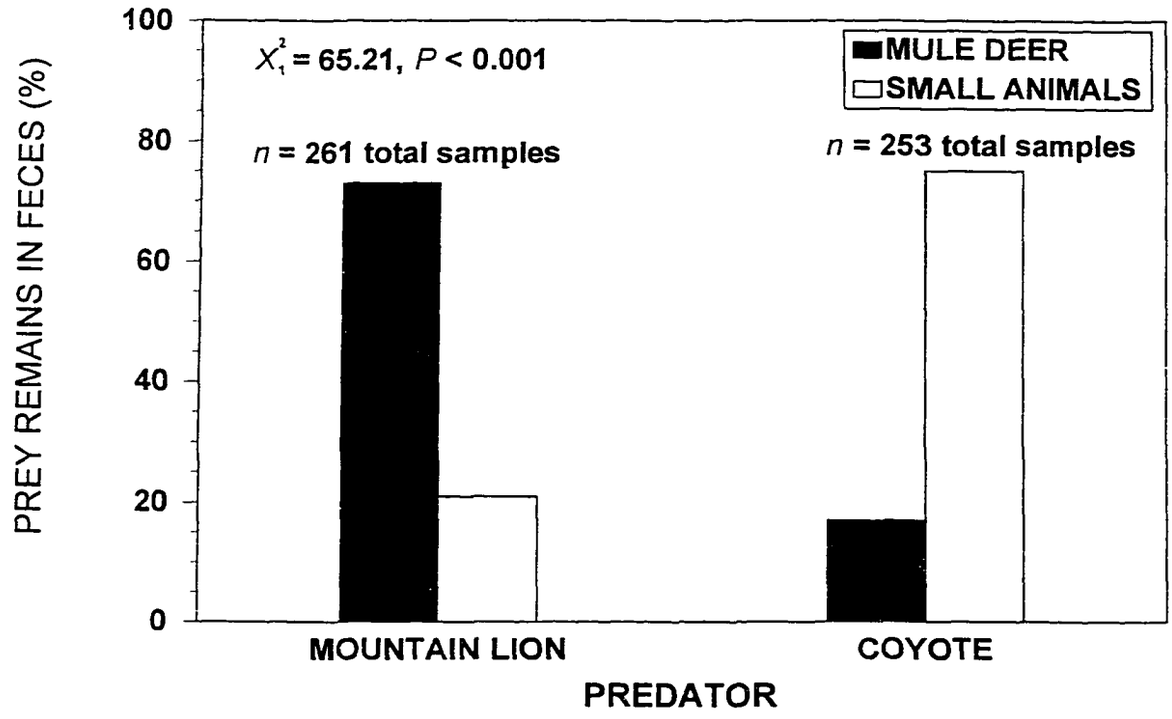

Fig. 4.1. Percent occurrence of remains of mule deer and small animals (< 15 kg) in the feces of mountain lions and coyotes; samples were collected from the eastern Sierra Nevada of California (1991-1998). Mule deer were an important component of the diet of mountain lions, whereas smaller animals, especially leporids, were most abundant in the diet of coyotes.

their winter range. Additionally, the percent of fat in the bone marrow of mule deer collected in March (78%) did not differ from the percent observed for adult females killed by vehicles in March (64%; $F_{1,36} = 2.70$, df = 1, $P = .10$). Analysis for deer killed during all months indicated that more young deer in the population were in poor condition than were adults ($P < 0.05$; Fig. 4.2); however, no selection occurred in the proportion of deer in poor condition killed by predators or by automobiles among young deer or adults (Table 4.1). In addition, mule deer in poor condition composed a small proportion of the deer killed by all sources (Table 4.1).

Analysis of age, sex, and condition of mule deer killed by automobiles, mountain lions and coyotes from October to June indicated no difference in the sex or condition of mule deer when adults and young were combined (Table 4.2). Mountain lions, however, killed significantly more young deer than did automobiles ($P < 0.01$; Fig. 4.3). Coyotes did not select more young (26%) than those killed by automobiles (21%; $P = 0.42$; Fig. 4.3). When comparing sex and age of adult mule deer among sources of mortality, mountain lions and coyotes killed more females than did automobiles ($P < 0.05$; Fig. 4.4), and the mean age of adult deer killed by predators was significantly greater than those killed by automobiles ($P < 0.001$; Fig. 4.5).

Mean weight ($\pm$ SD) of eight male mountain lions (56 kg $\pm$ 7.7) was > 25% the mean weight of eleven females (40 kg $\pm$ 5.1). Social categories of mountain lions did not differ in the sex or condition of deer they preyed upon, or from deer killed by automobiles when age categories of deer were combined (Table 4.3). Among adult deer, however,

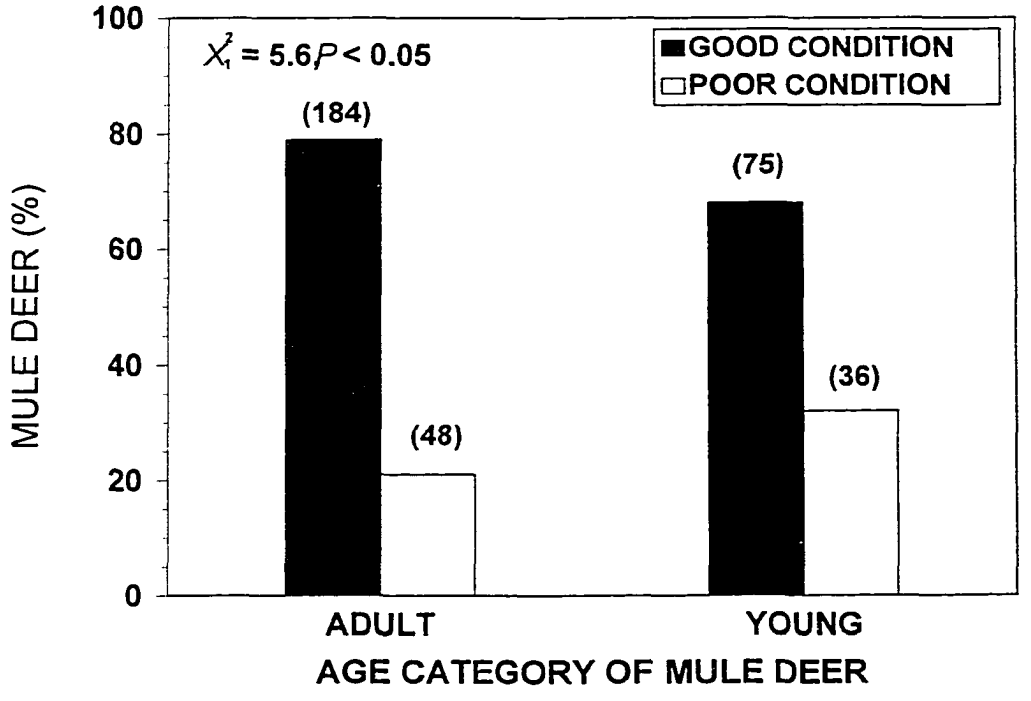

Fig. 4.2. Proportion of adult and young (< 1 year) mule deer from the eastern Sierra Nevada, California, in two categories of condition (1991-1998). Condition category was determined by percent fat in the marrow of femurs: good condition (> 50%), and poor condition (≤ 50%). Sample sizes are shown in parentheses.

Table 4.1. Proportion of mule deer in poor (≤ 50% bone marrow fat) and good (> 50% bone marrow fat) condition from different age categories killed by varying causes in the eastern Sierra Nevada, California, USA (1991-1998). Proportions were not significantly different among sources of mortality for young deer ($X^2 = 0.29$; df = 2; $P = 0.87$) or adults ($X^2 = 0.52$; df = 2; $P = 0.77$).

	Age category and physical condition of deer					
	Adult (≥ 1 year)			*Young (< 1 year)*		
Source of mortality	*n*	*Good(%)*	*Poor(%)*	*n*	*Good(%)*	*Poor(%)*
Automobiles	106	80	20	24	50	50
Mountain lions	99	80	20	74	69	31
Coyotes	27	74	26	13	62	38

Table 4.2. Proportion of mule deer killed by varying causes that were in poor (≤ 50% bone marrow fat) or good (> 50% bone marrow fat) condition or were female, in the eastern Sierra Nevada, California, USA (1991-1998). Data collected during July-September were excluded because of a high proportion of post-natal deer (< 4 months old) in the population that were not reflected in mortalities caused by vehicles. Proportions were not significantly different among sources of mortality for condition (X^2 = 1.48; df = 2; P = 0.47) or sex (X^2 = 2.97; df = 2; P = 0.23).

	Condition and sex of mule deer killed during October - June					
	Condition Category			*Sex*		
Source of mortality	*n*	*Good(%)*	*Poor(%)*	*n*	*Male(%)*	*Female(%)*
Automobiles	101	81	19	144	38	62
Mountain lions	157	78	22	152	36	64
Coyotes	43	72	28	46	24	76

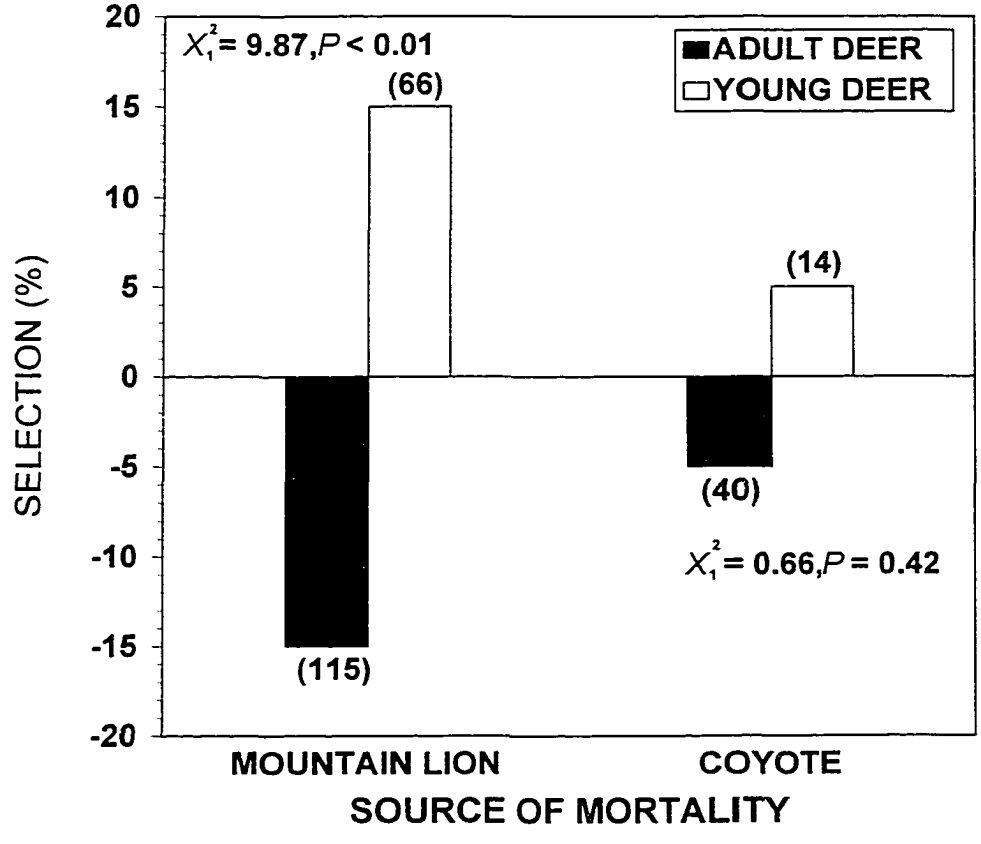

Fig. 4.3. Proportion of young (< 1 year) and adult deer killed by mountain lions and coyotes (October-June), in the eastern Sierra Nevada, California (1991-1998). Proportion of deer killed by predators, in both age categories, was compared with the proportion available in the population as indexed by deer killed by automobiles (0 on *y*-axis; % selection = % use - % available). Mountain lions preferentially killed young deer, whereas coyotes did not exhibit selection for either age class. Sample sizes are shown in parentheses.

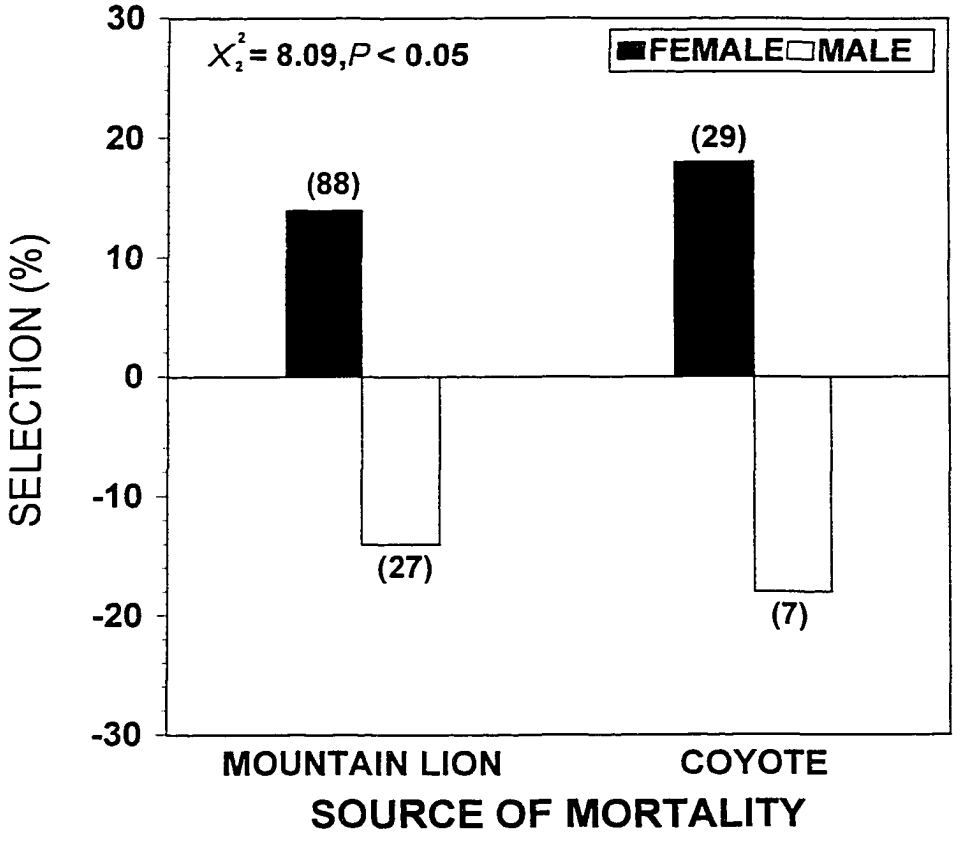

Fig. 4.4. Proportion of adult male and female mule deer killed by mountain lions and coyotes in the eastern Sierra Nevada, California (1991-1998). Proportion of each sex of mule deer killed by predators was compared with the proportion available in the population as indexed by deer killed by automobiles (0 on the *y*-axis; % selection = % use - % available). Both mountain lions and coyotes selected for female mule deer among adults. Selection for female deer by mountain lions was driven by female mountain lions. Sample sizes are shown in parentheses.

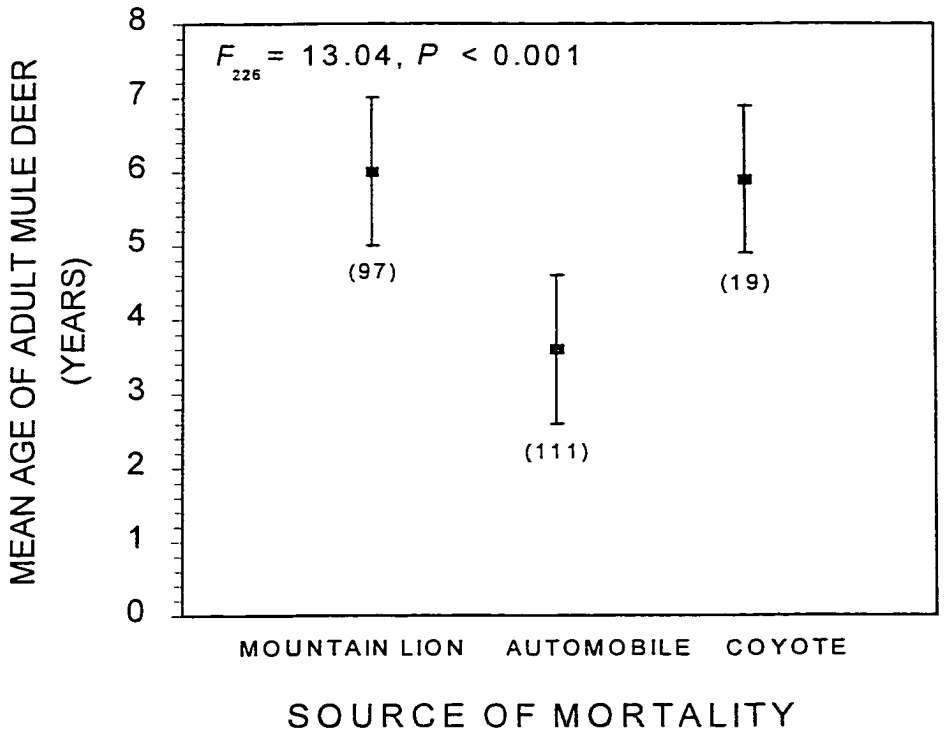

Fig. 4.5. Mean (± SE) age of adult mule deer killed by mountain lions, coyotes, and automobiles in the eastern Sierra Nevada, California (1991-1998). Ages of deer were determined by analysis of cementum annuli. Mountain lions and coyotes preyed on older adults when compared to adults killed by automobiles. Sample sizes are shown in parentheses.

Table 4.3. Proportion of mule deer killed by varying causes that were in poor (≤ 50% bone marrow fat) or good (> 50% bone marrow fat) condition or were female, in the eastern Sierra Nevada, California, USA (1991-1998). There was no significant difference in the condition ($X^2 = 3.58$; df = 4; $P = 0.47$) or the sex ($X^2 = 5.91$; df = 4; $P = 0.21$) of mule deer killed by mountain lions and those killed by automobiles when all age categories and all months were combined.

	Condition and sex of mule deer killed by mountain lions and automobiles					
	Condition Category			*Sex*		
Source of mortality	*n*	*Good(%)*	*Poor(%)*	*n*	*Male(%)*	*Female(%)*
Automobiles	132	78	22	111	40	60
(Social category of mountain lion)						
Solitary males	22	77	23	25	34	76
Solitary females	47	68	32	57	38	72
Females with Juveniles	28	86	14	22	41	59
Females with kittens (≤ 6 months old)	37	73	27	32	47	53

social categories that included females exhibited selection for female deer (79%; X^2 = 6.02; df = 1, $P < 0.05$) when compared with deer killed by automobiles (63%), but that difference was not significant for male mountain lions (81%; $X^2 = 2.70$; df = 1; $P = 0.10$). Social categories of mountain lions that included females killed significantly more young deer than did male mountain lions ($X^2 = 4.81$; df = 1; $P < 0.05$; Fig. 4.6) or automobiles ($X^2 = 31.01$; df = 1; $P < 0.001$; Fig. 4.6). When solitary females were analyzed separately, those animals still selected more young deer than those killed by automobiles ($X^2 = 11.12$; df = 1; $P < 0.001$; Fig. 4.6); however, solitary females did not differ from male mountain lions in selection of age categories of deer ($X^2 = 1.18$; df = 1; $P = 0.18$; Fig. 4.6).

Despite the concordance between proportions of young deer killed by automobiles from October to April and proportions observed in annual surveys, comparison of the proportion of young deer killed by automobiles (15%) and the estimated proportion of young deer based on fetal rates (51%) in late summer indicated that postnatal deer were under-represented in our sample of deer killed by automobiles ($X^2 = 21.70$, df = 1, $P < 0.001$). Although the proportion of postnatal deer in the population during late summer was likely over-estimated from fetal rates, female mountain lions with kittens still selected postnatal deer (92%) during late summer, when compared with the proportion of postnatal deer estimated by fetal rates ($X^2 = 7.94$; df = 1; $P < 0.01$).

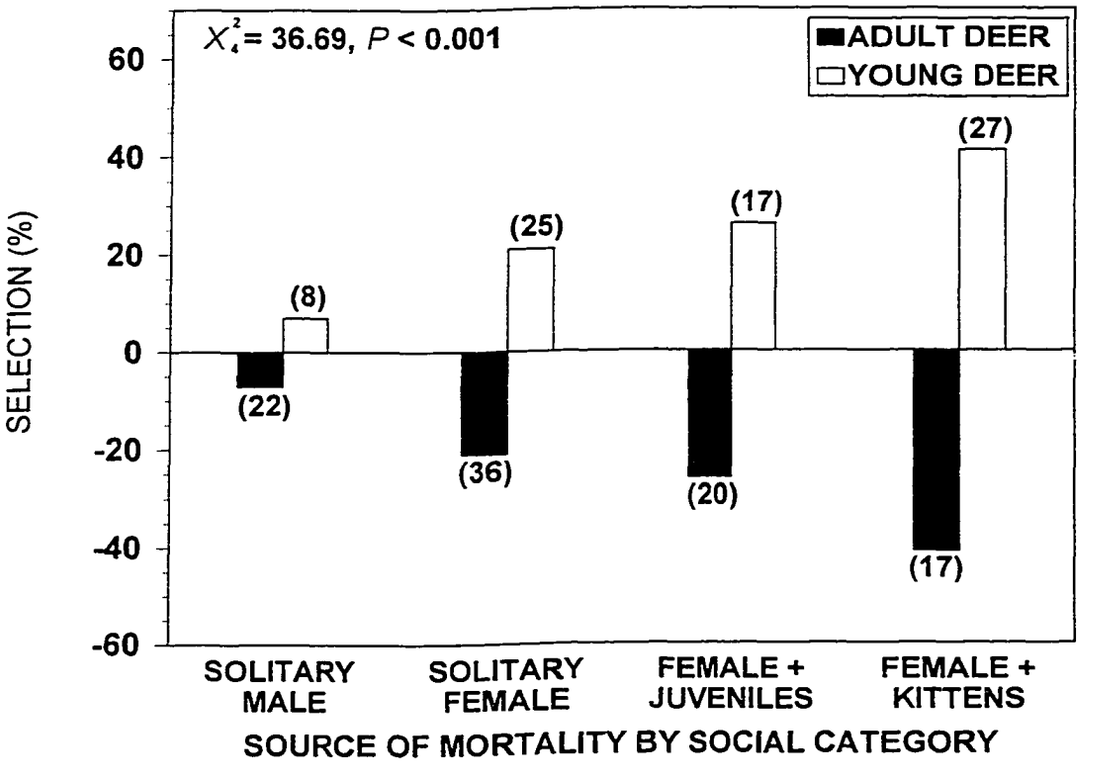

Fig. 4.6. Proportion of young (< 1 year) and adult deer killed by mountain lions in different social categories in the eastern Sierra Nevada, California (1991-1998): solitary males, solitary females, females with juveniles (> 6 months old but not independent), and females with kittens (≤ 6 months). Proportion of young and adult mule deer killed by each social category of mountain lion was compared with the proportion available as indexed by deer killed by automobiles (0 on *y*-axis; % selection = % use - % available).

Discussion

Hunting style was not an important factor in prey selection of mule deer by large carnivores because only mountain lions selected young deer (Fig. 4.3), but both mountain lions and coyotes selected older deer among adults (Fig. 4.5). Previous studies (Hornocker 1970, Spalding and Lesowski 1971) also reported similar results with mountain lions selecting young prey; predation on older age classes has been reported for wolves preying on white-tailed deer (*Odocoileus virginianus*; Pimlott et al. 1969), moose (Peterson et al. 1998, Mech 1970), caribou (*Rangifer tarandus*; Kuyt 1972) and Dall's sheep (*Ovis dalli*; Murie 1944). In addition, neither mountain lions nor coyotes selected individuals with low percentages of bone marrow fat. That outcome indicates that predation on mule deer was not selection for prey in especially poor body condition. The hypothesis that a stalking predator would not be selective in choosing prey was rejected because the mountain lions were as likely to select young prey as was the coursing predator (coyote).

The hypothesis that body size of the predator affects prey selection was supported both because mountain lions preyed on larger species of prey than did coyotes and mountain lions preyed more on adult mule deer. The smaller predator (coyote) had a significantly higher proportion of small prey in their diets than did the larger predator (mountain lion; Fig 1). Furthermore, female mountain lions, which are smaller than males, selected female deer, whereas male mountain lions did not. Selection of female deer by mountain lions was contrary to the findings of Hornocker (1970), but was

consistent with results from deer populations in the area surrounding our study (Bleich and Taylor 1998). Hornocker (1970) reported selection for male prey and proposed that male deer and elk (*Cervus elaphus*) were weakened during the mating season and therefore were more prone to predation by mountain lions. In addition, male ungulates also segregate from females seasonally (Bowyer 1984, Bleich et al. 1997), and may select habitats that are more risky in terms of predation than do females (Hornocker 1970, Bleich et al. 1997). The proportion of adult male deer on the winter range in Round Valley, as indexed by aerial surveys, increased during 1992-1997 from 12% to 45% of the adult population compared with 19% for the population of ungulates in Idaho (Hornocker 1970). The steady increase of male deer in the Round Valley population, during the course of our study, may indicate that a large proportion of the males available to mountain lions and coyotes in Round Valley were younger males that had not yet participated in strenuous mating activities, and were not in weakened physical condition.

Results of prey selection between young and adult deer for a small predator (coyotes), which weigh ca. 9.8-11.2 kg in California (Hawthorne 1971), and a larger predator (mountain lions) caused us to reject the hypothesis that body size primarily determines prey selection; coyotes did not select for young deer (Fig 4.3). That result also indicated that young deer, despite their smaller size, were not preferred by female mountain lions. We note, however, that our results were for October-July. Postnatal deer may have been under-represented in predator kills because fewer remains of young are left and their carcasses are more difficult to locate (Schaller 1967, Johnsingh 1993). No

deer killed by coyotes were located during late summer, and that outcome could be a result of coyotes completely consuming postnatal deer before we were able to locate carcasses. Coyotes have been reported to prey heavily on young deer in late summer in other studies (Litvaitis and Shaw 1980, Andelt 1985, Bowyer 1987). In addition, coyotes often hunted in packs in Round Valley (B. M. Pierce, personal observation) and elsewhere (Bowen 1981, Messier and Barrette 1982, Bowyer 1987), and may benefit energetically by killing larger prey when these carnivores are in large social groups (Kruuk 1975, Peterson 1977).

For female mountain lions rearing offspring, young deer were strongly selected as prey. Young deer may be easier to catch than adults because young lack experience in escaping predators or lack stamina (Curio 1976, Schaller 1972). Because protein is stored as muscle, drawing upon protein reserves for too long can affect locomotory function (Wannemacher et al. 1970). During lactation female mountain lions may need a more constant intake of protein than do males. We hypothesize that risk of an unsuccessful hunt and the accompanying drain on protein reserves may overshadow the benefit of killing larger prey for females that are lactating. Male mountain lions may have lower rates of predation, killing larger prey less often and gorging themselves to store fat. Such a strategy would allow males to make long-range movements in search of females and in defense of their relatively large territories (Anderson et al. 1992).

Sexual segregation in both predator and prey also may have led to differences in prey selection between age categories of deer, because female mountain lions with kittens

were located at relatively low elevations during the late summer, compared with other social categories of mountain lions (Pierce et al. in press). Male deer segregate from females with young during spring and summer (Bowyer 1984, Main and Coblentz 1996) and in consequence may have been encountered at low frequencies by mountain lions at lower elevations. The selection for young deer by mountain lions rearing offspring, however, was significant even when compared with the most conservative estimate of available prey.

Our study demonstrated that presence of dependent young was a critical factor affecting prey selection by mountain lions, whereas hunting style was not. Contrary to our prediction, the stalking predator was as selective as the coursing predator. Our tests of the hypothesis that body size was an important factor in prey selection were inconclusive. The body-size hypothesis was supported when we compared the selection of large and small animal species in the diets of mountain lions and coyotes. In addition, sex of mule deer preyed upon by adult male and female mountain lions, and all social categories of female mountain lions, demonstrated selection for young deer, whereas solitary males did not select that age class. Body size, however, did not affect prey selection by mountain lions between adult and young mule deer when solitary males and solitary females were compared. Furthermore, the smaller species of predator did not select for young deer. This may be the result of pack hunting by coyotes (Bowen 1981, Bowyer 1987) which could have allowed them to take larger prey without a considerable increase in risk. Size ostensibly allowed the largest predator (male mountain lions) to

take prey as it was encountered, whereas smaller predators were more selective. Nonetheless, presence of dependent young rahter than size was more important in determining prey selection.

Other investigations (Mech 1970, Hornocker 1970, Mech and Frenzel 1971) have reported results similar to ours for prey selection among multiple species of prey or by a single species of predator. Our study, however, is unique in that we tested hypotheses concerning the effects of hunting style, body size, and reproductive status in large carnivores on selection of a single prey species (mule deer). Our results emphasize the importance of considering reproductive status of the predator when attempting to predict the effects predation may have on selection of prey. Further study of the effects of energy demands caused by reproduction on prey selection by carnivores is needed to understand predator-prey relationships more completely.

Acknowledgments - We thank the houndsmen, field technicians, and volunteers that helped capture mountain lions and to locate deer killed by mountain lions: J. Davis, V. Davis, J. Ostergard, C. Baker, P. Partridge, C.-L. Chetkiewicz, G. Raygorodetsky, and D. Stoner. Special thanks to J. Wehausen for assistance in capturing mountain lions. We also are grateful to the volunteers who helped in daily monitoring of the deer herd: W. Allsup, C. Baker, G. Clarkson, H. Jones, R. Noles, D. Noles, N. Partridge, P. Partridge, B. Peters, P. Thompson and, the late, R. Williamson. We extend special thanks to pilot R. Anthes for his safe flying. This research was supported by the California Department

of Fish and Game (CDF&G), The National Rifle Association, Friends of the National Rifle Association, The Mule Deer Foundation, Safari Club International (Los Angeles, Orange County, Sacramento, San Fernando, and San Francisco Bay Area chapters), the Fish and Game Advisory Committee of Inyo and Mono Counties, the California Deer Association, University of California White Mountain Research Station, and the Institute of Arctic Biology at the University of Alaska Fairbanks. This is a contribution from the CDF&G Deer Herd Management Plan Implementation Program and is Professional Paper 15 from the Eastern Sierra Center for Applied Population Ecology.

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SYNOPSIS AND CONCLUSIONS

The movements of mountain lions that winter in Round Valley, California raised questions about the potential for mountain lions to self-regulate their numbers through social interactions and territoriality. Migrations made by individual females, in response to food availability, led to seasonal changes in population densities, suggesting that the prey population was the most important factor regulating mountain lion densities. Furthermore, the population of mountain lions wintering in Round Valley severely declined following the decline in the mule deer population, indicating that the mountain lion population had not been held far below carrying capacity by social regulation. Examination of social interactions between individual pairs of mountain lions further supported the conclusion that territoriality was not limiting the mountain lion population through exclusive use of prey resources, and, therefore, it was unlikely that social regulation was operating in this system.

Our observations that mountain lions in Round Valley migrate seasonally, and are not territorial, have important implications for the conservation of mountain lion populations. Migratory behavior must be considered when managers attempt to estimate numbers of mountain lions, especially if track censuses are used, because sampling in different seasons can greatly influence results. Migration corridors also must be considered when managers are determining habitat use and minimum requirements for mountain lion populations. Finally, the management of mountain lion populations can not rely on the presumption that all are self regulatory. The densities of some mountain

lion populations may ultimately depend on the densities of their food supply, as noted for many other predator-prey systems. Thus, populations of mountain lions may have the ability to reach and deplete the carrying capacity of their prey base and, thereby, have important impacts on prey populations.

The distributions of mountain lions and mule deer influence each other not only at the level of the landscape, but also at the scale of the microhabitat. Mountain lions are significant predators on mule deer, and, therefore, habitat selection by mule deer most likely evolved in response to predation by mountain lions. Our results, indicate, however, that mule deer that forage on winter ranges in the Great Basin do not face a trade-off in forage benefits and predation risk from mountain lions. The safest habitat in which mule deer feed, bitterbrush habitat, is also the one that provides the best forage; therefore, mountain lion predation probably does not influence populations of mule deer in Great Basin habitat indirectly through limitation of food resources on winter ranges.

Finally, previous studies have suggested that the effects of predation on ungulate populations may involve several factors, including hunting style, body size, and demography of the predator population. For mule deer in Round Valley, our results indicate that the differences between coyotes and mountain lions in hunting style and body size do not affect the condition, sex, or age class of mule deer killed by these predators. Mule deer, among these different categories, however, are not killed in the proportion in which they occur in the population. Coyotes and mountain lions both selected females and, among adult mule deer, older age classes. Furthermore, female

mountain lions with dependant young strongly selected mule deer < 1 year old. Therefore, managers attempting to predict the influence of predators on mule deer populations need to consider the demography of both predator and prey populations in their models.

Research on predators has often failed to consider the distributions, behavior, and demography of the populations of prey. This is especially true for large mammals in North America, including studies of mountain lions and their primary prey, deer. The lack of studies that have monitored predators and prey simultaneously may be the result of increased costs incurred in the study of two populations instead of one. For researchers and managers, however, it is important to recognize that conclusions drawn about predators, in the absence of data on critical prey populations, will likely contribute little to an overall understanding of the system. The influence of predation can be interpreted correctly only by considering the characteristics of both the predator population and the prey population at the same time.